

***Cowralepis*, a new genus of phyllolepid fish (Pisces, Placodermi) from the Late Middle Devonian of New South Wales, Australia**

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Cowralepis mclachlani, a new genus and species of phyllolepid placoderm (Pisces, Placodermi), is described from numerous articulated specimens discovered near Cowra, New South Wales, Australia. *Cowralepis*, represented by a growth series, illustrates ontogenetic changes from juvenile to adult and throws new light on the dermal, endocranial, visceral and axial skeleton of phyllolepid and on placoderm interrelationships. The head shield is longer than the trunk shield, the reverse of the situation in other phyllolepid genera. The presence of two pairs of upper tooth plates, plus a posterior dorsolateral plate, an anterior median ventral plate and one or more posterior median ventral plates in the trunk shield is confirmed. The phyllolepid jaw apparatus and associated structures, first reported in *Austrophyllolepis*, are reinterpreted. The branchial skeleton, an occipital ossification and a fused synarcual, previously unknown in phyllolepid, are described. *Cowralepis* had an ossified vertebral column, a large epicercal caudal fin and small pelvic fins but lacked a dorsal fin. The *Cowralepis* material has suffered regional tectonism and illustrates why tectonic deformation must be taken into account in the interpretation of fossils from ancient fold belts.

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INTRODUCTION

In January 1993, during the preliminary excavation of a major Late Devonian fish site near Canowindra, New South Wales (Ritchie in press), the late Mr Reg Dumbrell, a Canowindra resident, showed the writer some Devonian fish specimens he had collected from another site, about 15 km south, in Cowra Shire. Dumbrell's best find, on a piece of black shale 10 cm square, was a small, articulated armoured fish, a phyllolepid, with the tail of a second individual lying beside it. Articulated phyllolepid had previously been recorded from only two sites in the world – Dura Den, Fife, Scotland, and Mt Howitt, Victoria, Australia.

The source of Dumbrell's find was unexpected; the margins of the approach roads to Merriganowry Bridge, a causeway over the Lachlan River, 20 km northwest of Cowra, NSW, and about 2 km from any natural rock outcrop. In March 1993 the writer and

colleagues visited the site, located more fish fossils and solved the mystery. The fish-bearing black shale was not *in situ*. It had been quarried elsewhere, trucked in and crushed for road-base material - the local roads were literally paved with fossil fish!

Cowra Shire Council confirmed the source to be a small quarry 2 km from Merriganowry Bridge, just north of Merriganowry Hall and only 50 metres east of the main road from Cowra to Forbes (Young 1999, fig.1B, locality 6). This quarry, on private land, had been worked on and off for 10-15 years, apparently without anyone noticing, or at least reporting, the presence of abundant, well-preserved fossil fishes in the shale.

With permission of the new landowner, Mr Alex McLachlan, the writer first visited Merriganowry in June 1993 and uncovered a fossil treasure trove. Some sixty phyllolepid specimens, large and small, many complete with tails, were recovered by the writer in three days digging! At a conservative estimate, tens

or hundreds of thousands of fossil fish specimens had been quarried from this site and crushed for road material before its scientific importance was recognised.

When informed of its unique scientific importance, Mr McLachlan immediately arranged for the quarry to be secured and fenced, at considerable cost, and made it available to the Australian Museum for long-term, systematic investigation under scientific supervision. Since September 1993 the Merriganowry site has been excavated by paying volunteer groups supervised by the writer and Dr Zerina Johanson from the Australian Museum and organised by an eco-tour operator, Monica Yeung, Gondwana Dreaming Inc., of Canberra.

All of the material collected by these groups has been retained for scientific study and deposited with the Australian Museum, providing a unique scientific research resource. Several hundred fish specimens have been recovered from Merriganowry, many of them articulated individuals complete with tails, and they represent a continuous growth series from juveniles 5 cm long to adults over 35 cm long. Strangest of all, after 11 years of supervised group digs, every fish fossil recovered from Merriganowry (with the exception of dissociated scales in associated coprolites) appears to belong to a new genus of phyllolepid placoderm, *Cowralepis*.

Phyllolepids were dorsoventrally flattened placoderms with a distinctive, sub-concentric ridged ornament, hence their name meaning 'leaf-scale'. Most phyllolepid finds consist of dissociated or fragmentary dermal bony plates; articulated specimens are extremely rare, which is why the Merriganowry site is so important.

Most of our previous knowledge of phyllolepids comes from three genera: *Phyllolepis* from the Late Devonian of the Northern Hemisphere, and *Austrophyllolepis* Long, 1984 and *Placolepis* Ritchie, 1984 from the Middle-Late Devonian of Australia; for reviews of earlier phyllolepid discoveries see Long (1984 263-4) and Ritchie (1984 321-3). Many of the new phyllolepid discoveries since 1984 have come from Gondwanan sites. In Australia these include the Amadeus and Georgina Basins, central Australia (Young 1985, 1988, in press a), southeastern New South Wales (Young in press b), Victoria (Long 1989) and Queensland (Turner et al. 2000). Phyllolepids have also been described from Antarctica (Young 1989, 1991; Young and Long in press), Venezuela, South America (Young et al. 2000; Young and Moody 2002) and Turkey (Janvier 1983). Articulated phyllolepids have also recently been reported from Pennsylvania,

U.S.A. (Daeschler et al. 2003).

Phyllolepid fishes have not yet been recorded either from Asia, where diverse fossil fish assemblages of appropriate age are extensively documented, or from Africa.

GEOLOGICAL SETTING

Horizon and age.

The phyllolepids described here all come from the Merriganowry Shale Member that was uncovered by quarrying for road-base material in the 1980's and early 1990's. The more resistant outcrops (rhyolitic volcanics) forming the east margin of the quarry had initially been mapped as part of the Canowindra Volcanics, of possible Silurian age. The quarry exposed a conformable relationship between the fish-bearing black shales and underlying volcanics, showing that the latter must also be Devonian in age, not Silurian.

Young (1994, 1999, figs 2, 3) correlated the volcanic sequence at Merriganowry with the much younger Dulladerry Volcanics, which crop out over a large area of NSW between Narromine, Dubbo, Forbes and Bathurst and underly the Late Devonian Hervey Group on the western edge of the Hervey Syncline. The youngest Dulladerry Volcanics are now estimated to be Late Middle Devonian in age (Givetian), which would date the Merriganowry black shales as either Late Givetian or Early Frasnian (Young 1999, fig. 5B). This is consistent with the fish and associated palaeobotanical evidence.

No direct contact has been identified between the west-dipping shale and volcanic sequence at Merriganowry and the overlying Hervey Group, but sandstone ridges 1 km north of Merriganowry quarry, with the same strike and dip, have been mapped as Peaks Sandstone, the basal unit of the thick Hervey Group, suggesting a conformable sequence between them.

Although the very limited exposure of the Merriganowry Shale Member precludes a total thickness estimate, its exposed lower section, directly overlying the volcanics in Merriganowry quarry, dips at 45° to the WSW (245°), and the fish-bearing sequence is estimated to be at least 25 metres thick. Excavations over the past 12 years have confirmed the presence of fish remains on hundreds of different bedding planes throughout the sequence, from just above the underlying volcanics to the top of the section exposed in the quarry.

Environment of Deposition.

Young (1999, 144; P. O'Brien, pers. comm. 1994) reported that "the locality is a black shale deposit closely associated with the underlying volcanoclastics including rhyolite blocks and possible flows. The shale includes slumped beds and graded interbeds of rhyolitic sand up to 30 cm thick, suggesting deposition in a lake of sufficient size and depth for turbidity currents to be generated, with water depths of tens to hundreds of metres, perhaps an elongate deep lake such as are associated with strike slip faulting."

Krynen (in Pogson and Watkins 1998, 224-5), in formally naming the Merriganowry Shale Member, noted "this sequence suggests initial subaerial outwash fan deposition in a volcanic rift setting passing upwards to turbiditic deposition in a deep lake environment following at least local cessation of volcanism. The formation of the lake may have been associated with strike-slip faulting within the volcanic rift."

Associated fauna and flora

The Merriganowry fauna is extremely restricted. The only identifiable fish remains, recovered after 11 years of systematic collecting with the assistance of many hundreds of volunteers, almost all appear to belong to one genus of phyllolepid, *Cowralepis* gen. nov., described here. A few fragments of eurypterid integument have been recovered from one layer high in the section. Apart from these, the only other fossils recovered are fragmentary plant remains including lycopods (*Protolepidodendron*) and branching stems (cf. *Prearamunculus*) and what appears to be an egg sac (Fig. 18D).

What the abundant phyllolepids ate remains a mystery - probably plant debris and small invertebrates not preserved as fossils. Coprolites up to 20 mm long, presumably derived from the dominant phyllolepids, are common throughout the Merriganowry section but are invariably deeply weathered. When cleaned out, these may reveal traces of their contents, but preserved only as natural moulds. They include comminuted bone fragments, some of which appear to be of phyllolepid origin, and several coprolites contained abundant minute scales, about the size and shape of thelodont denticles, but not well enough preserved to be identifiable.

It appears unlikely that the phyllolepids lived on the bottom of the lake because the shale layers are generally smooth, flat and undisturbed, free of burrowing organisms and with very few trace fossils. The abundance of articulated phyllolepid specimens complete with delicate tails indicates an absence of

scavengers and suggests that the bottom conditions were probably anoxic.

The observation that about half of the dorsoventrally flattened phyllolepids found *in situ* at Merriganowry were buried upside down suggests that they probably lived in the upper, better-oxygenated water levels and only after death fell randomly to the bottom where they lay undisturbed until covered. The same conditions must have persisted for many thousands of years as the shale deposit slowly accumulated, during which time the fauna was dominated by phyllolepid fishes to the virtual exclusion of all other groups.

The Merriganowry fauna, and the conditions under which it lived and was buried, thus presents a sharp contrast with the Late Devonian mass-kill fish site discovered only a few kilometres to the north, near Canowindra, New South Wales (Ritchie in press). The Canowindra assemblage of placoderms and sarcopterygians, dominated by two antiarch genera, *Bothriolepis* and *Remigolepis*, comes from a single bedding plane on which many thousands of fishes lie crowded tightly together, almost all of them (about 95%) buried right way up. Canowindra represents a unique time capsule, a sample of a single population killed and buried quickly as the result of a local environmental disaster, probably an extreme drought.

MATERIAL AND METHODS

Note: to facilitate cross-referencing of specimens all figures are located at the end of the paper from page 240

The original bone was often preserved but deeply weathered and was removed by washing, by airbrasures, mechanically or with dilute hydrochloric acid. The resulting detailed natural moulds (negatives) were cast using black-pigmented latex rubber. The latex casts were whitened with ammonium chloride sublimate and photographed with a Nikon Coolpix digital camera. Most of the images used here show the original uncorrected dimensions, with the exception of several specimens (Figs 6a-D, 9F, 10H, 11B, 16A-C) in which these have been digitally modified, as indicated, using Adobe Photoshop LE, to correct for the effects of regional tectonic deformation.

Silicone rubber moulds were prepared from the latex casts (which have a limited shelf life) and most of the figured specimens have been replicated as resin casts (positives) for collection and study purposes and for scientific exchange with other institutions.

Interpreting tectonically deformed fossils – the long and the short of it.

Not only do the Merriganowry phyllolepid represent a very wide growth range, from juveniles to adults, but they also display considerable variation both in relative proportions and in ornament (Fig. 2). Some specimens are deceptively symmetrical (Fig. 5), but most show visible evidence of deformation and/or asymmetry.

They confirm a) that the Merriganowry Shale Member had undergone significant shear strain, b) that the fish fossils provide a means of directly measuring this and c) that much of the morphological variation and deformation at Merriganowry can be attributed to post-mortem tectonic deformation, which must be taken into account in interpreting such material.

Many of the fossils found in areas subjected to major regional tectonism are distorted, a phenomenon documented for many types of fossils since the mid-19th century. Ramsay and Huber (1983, 127-149) illustrated how tectonically deformed fossils (trilobites, brachiopods, corals, graptolites, ammonites etc.) could provide structural geologists with a useful method of strain measurement. Graphical techniques developed for restoring deformed fossils have mostly been used for invertebrates and plants (Cooper 1990) but less often for vertebrates.

Tectonic strain is most readily detected in fossil organisms that were originally bilaterally symmetrical, where the original axis of symmetry can only lie in two directions, at right angles on the bedding plane without any loss of symmetry. Such organisms (the Welsh Ordovician trilobites, *Angelina* and *Bathyriscus* are classic examples) provide the simplest subjects for study (Ramsay and Huber 1983, figs 8.7, 8.8). Where the original shape of these fossils is already known it can be used to determine the shear strain in deformed specimens and restore them to their original shape. Dorsoventrally flattened (and bilaterally symmetrical) armoured fishes such as phyllolepid provide ideal subjects especially where, as at Merriganowry, innumerable specimens were buried articulated and undisturbed *post mortem*.

Despite the widespread use of length/breadth ratios and angular measurements in the description and classification of fossil vertebrates, such correction techniques have rarely been applied to fossil vertebrates. Failure to recognise, and correct for, tectonic deformation has undoubtedly led to misidentification of fossil species and proliferation of invalid taxa.

Because most of the *Cowralepis* specimens were discovered only **after** blocks had been excavated for splitting by volunteers, their original orientation

in the ground had been lost. A small number of *Cowralepis* specimens were found *in situ* (<5%) as the outcrop was excavated and their orientation could be measured before removal.

The extremes of deformation displayed by *Cowralepis* specimens from Merriganowry are illustrated by two types of specimens displaying bilateral symmetry - **broad symmetric** and **narrow symmetric** - depending on whether the broad symmetry axis is parallel to the long or to the short axis of the strain ellipse (Fig. 5A-D). Such specimens cannot be used to determine shear strain. Most of the phyllolepid from Merriganowry are visibly asymmetric, or skewed, to various degrees, and appropriate correction techniques need to be applied.

Digital reconstruction of deformed fossils.

The first step is to determine the direction of **greatest principal extension** (GPE) and **smallest principal extension** (SPE) of the fossil. At Merriganowry the GPE coincides approximately with the strike direction of the steeply dipping shale layers and the SPE lies at right angles to it, up-dip and down-dip. *Cowralepis* specimens discovered *in situ* are marked with strike and dip directions before removal (Fig. 3B).

In specimens where the original orientation of the specimen has been lost the GPE orientation may be determined from prominent directional wrinkling of the smooth bony plate surfaces. This marks the intersection of the axial plane cleavage with the bedding plane (Figs 1A, 4A, 5A-D, 11A, 14A), and its orientation can be estimated to within a few degrees.

Where such surface wrinkling is not well developed, the GPE can be identified using standard techniques used by structural geologists for determining first generation cleavage and incipient cleavage in clastic rocks of low to very low metamorphic grade (Durney and Kisch, 1994). Dr David Durney, Macquarie University, visited Merriganowry with the writer to advise on their use in determining the GPE of *Cowralepis* specimens.

Using graphical methods described by Ramsay and Huber (1983, fig. 8.5, Breddin curve) and Cooper (1990, fig. 5, Wellman's method - deformed right angles) the degree of shear strain at Merriganowry was estimated. It was then tested on several examples in which two *Cowralepis* specimens were recovered lying close together on the same bedding plane but in different orientations. The availability of modern computers and digital image processing programmes makes this process much easier. After trial and error, the approximate degree of correction required to bring both specimens back to symmetry, and to the

same proportions, was determined and this has since been applied to many single *Cowralepis* specimens (Figs 6A-D, 9E, F, 10G, H, 11A, B).

When the GPE had been determined, a digital image of the fossil (or cast) was rotated until the GPE was horizontal. Using Adobe Photoshop the image was then reduced by 10% in the direction of GPE and increased by 10% in the direction of SPE. Reducing the GPE and increasing the SPE by the same amount produces a corrected image with approximately the same surface area as the deformed original (Figs 9F, 10H, 11B; strain directions indicated by arrows with percent correction indicated).

How many species?

The remarkable range of morphological variation in phyllolepid from Merriganowry raises the question – how many species are present at this site? If the specimens illustrated here (cf. Figs. 2, 5) had been recovered from several different sites, how many ‘species’ or even ‘genera’ of phyllolepid might have been erected?

Many factors are involved: the presence of unique characters and morphological variation (breadth/length and angular measurements); variation in ornament; extent and direction of sensory canal grooves; differential changes during growth (allometry); differential changes through time (heterochrony); differences in preservation (selective diagenesis); sexual dimorphism; sample size, and whether the sample comes from one horizon or from different levels; and, where relevant, tectonic deformation.

This is illustrated by the problems encountered in interpreting phyllolepid material from three widely separated Devonian sites in southeastern Australia – Mount Howitt, Victoria (Long 1984), Nettleton’s Creek, New South Wales (Ritchie 1984) and Merriganowry, New South Wales (this paper).

The Mount Howitt fauna, excavated by Monash University teams in the 1960’s and 70’s, comprises a diverse assemblage of late Middle Devonian fishes (placoderms, acanthodians, sarcopterygians, actinopterygians) represented by hundreds of articulated specimens in all stages of growth. These include a small number of placoderm specimens described by Long (1984) as a new genus of phyllolepid, *Austrophyllolepis*, represented by two species, *A. ritchiei* and *A. youngi*. (1984, figs 8 and 13 respectively)

Long (1984, 274) differentiated *A. ritchiei* (fig. 7) from *A. youngi* (fig 13) “. . . only by the proportions of the dermal armour (figs 8, 25), specifically the preorbital, paranuchal, nuchal, median dorsal, anterior and

posterior ventrolateral plates. Although the ornament appears to be more finely developed in *A. youngi* relative to *A. ritchiei* it is not a distinguishing feature for the species as a whole.” *A. ritchiei* was shorter and wider and *A. youngi* was longer and narrower, but otherwise there was very little to separate them.

Long (1984, fig. 8) also analysed proportional differences in the breadth/length index of the nuchal and median dorsal plates of *Austrophyllolepis*, based on a small sample of 23 specimens. These appeared to fall into two distinct clusters for each plate, with no overlap, and were interpreted as support for two species of *Austrophyllolepis* at Mt Howitt.

The writer suspected this interpretation might be incorrect after examining several specimens of *Austrophyllolepis* from Mt Howitt in the Australian Museum collection (not included in Long’s sample), some of which, when measured, fell between the ranges shown for *A. ritchiei* and *A. youngi*. Casts of the figured specimens of *A. ritchiei* (Long 1984, figs 3, 4) and *A. youngi* (1984 fig. 9) showed the same signs of deformation as those seen in phyllolepid from Merriganowry (asymmetry, surface wrinkling aligned in the direction of GPE) indicating that the Mt Howitt phyllolepid had also experienced tectonic deformation.

The computer image correction techniques used on Merriganowry phyllolepid were applied to the Mt Howitt specimens with similar results. The *Austrophyllolepis ritchiei* specimens became longer, narrower and symmetrical and the *A. youngi* specimens became shorter, broader and symmetrical.

Long later admitted (1999, 36) “. . . that there may only be one species present, as deformation of the strata can account for the distortion of plate measurements that separate the two originally named species.” The hypothesis that only one species of *Austrophyllolepis* is present at Mt Howitt can be readily tested by the recovery and analysis of additional *Austrophyllolepis* material from the Mount Howitt site, which is still accessible, and checking whether the deformation present in the fossils is directly related to regional tectonism.

A similar wide range in length/breadth proportions was also observed in the head and trunk plates of another phyllolepid, *Placolepis budawangensis* Ritchie (1984), from Nettleton’s Creek, NSW described at the same time as *Austrophyllolepis*. This was especially noticeable in the nuchal plates (1984, figs 4, 5). Several ventral trunk shield plates, found closely associated on the same bedding plane (but lying in different orientations), probably came from one individual. They displayed similar ornament but differed markedly in shape and proportions (1984, fig.

11). This was attributed to post-mortem deformation caused by regional tectonism. All of the material came from one small excavation about two metres square in a creek bank, and from the same siltstone unit. The writer concluded that only one species of *Placolepis* was represented in the Nettleton's Creek fauna.

The same applied to the associated material of *Bothriolepis longi* Johanson and Young (1999, figs 3, 5, 6). The presence of long/narrow and short/broad variants of *Bothriolepis* initially raised the possibility of two species being present (1999, 66) but this was dismissed. The morphological deformation at Nettleton's Creek is largely the result of regional tectonism.

In the analysis of tectonically deformed material, standard length/breadth ratios and angle measurements are of limited value. The writer applied the same length/breadth index method used by Long (1984, fig. 8) to *Cowralepis*, but based on a much larger sample - 143 nuchal plates and 124 median dorsal plates. The length/breadth distribution of both samples (not shown here) were similarly very widely scattered but not meaningfully clustered. It is clear that such graphs cannot be used to demonstrate the presence of one or more species in a fauna, especially where the specimens come from different layers and where tectonic deformation is involved, as at Merriganowry, Mount Howitt and Nettleton's Creek.

The articulated phyllolepid specimens from Merriganowry, covering a wide size range, made possible another approach. Unlike length/breadth ratios, plate ratios along the same axis are not altered by distortion, so the most useful plates for analysis are the large median plates in the head and trunk shield, the nuchal and median dorsal plates.

Eighty specimens (including many of the figured specimens) were selected in which both the nuchal and median dorsal plates remained in close association and lay in the same orientation. The length of each Nu and MD was measured separately along the midline and combined to provide data for the horizontal axis; the vertical axis illustrates the relative lengths of the nuchal and median dorsal plates (Fig. 3A.)

The eighty specimen points (Fig. 3A) are widely scattered, with little obvious clustering (other than an abundance of smaller individuals), and are of little use in determining whether one or more species of phyllolepid are present at Merriganowry. What they do appear to illustrate is a dramatic allometric change in the relative lengths of the *Cowralepis* head and trunk shields during ontogeny. This is discussed more fully in the description of the dermal skeleton.

Based on the material available for study, only one genus of phyllolepid placoderm appears to be

present at Merriganowry. *Cowralepis* gen. nov. displays a combination of characters not found in other phyllolepid genera. These include: head shield longer than trunk shield; only one pair of sensory canal grooves (central sensory line) crosses from circumnuchal plates onto the Nu plate; lateral line canal groove passes off PNu onto Mg plate between 78-92% of PNu length (intermediate between *Placolepis* and *Austrophyllolepis*); a fenestra is present between the PtO, Mg and PNu plates and the Nu plates (most noticeably in juvenile specimens); a small posterior dorsolateral plate is present under the lateral margins of the median dorsal plate.

The phyllolepid specimens from Merriganowry cover a wide size range and display a remarkable degree of morphological variation; they also come from many different levels within the Merriganowry Shale Member and thus represent a large and mixed sample covering a wide time span. Most importantly, every phyllolepid specimen from Merriganowry has been deformed, limiting the use of standard proportional length/breadth ratios for taxonomic determination.

While it is certainly possible that the material recovered from Merriganowry may well include more than one species of *Cowralepis*, it is **not** possible to confirm or refute this at present.

The course proposed here is to designate a single species, *Cowralepis mclachlani* sp. nov. to establish the new taxon in the realisation that it may include material from more than one species. It will take many more years of excavation, including the use of heavy equipment, to sample throughout the whole shale section at Merriganowry before the question of how many species are present can be tested. Twelve years of digging using many hundreds of volunteers has barely made a dent in the Merriganowry quarry, but this unique site has the potential for a long-term systematic research program, with educational and eco-tourism benefits as a bonus.

Abbreviations.

ADL, anterior dorsolateral plate; **AL**, anterior lateral plate; **AMV**, anterior median ventral plate; **ant ridge**, inner anterior ridge on AVL plate; **Art**, articular; **AVL**, anterior ventrolateral plate; **Bhy**, basihyal; **buttr AL**, buttress on inner surface of ADL plate, below AL plate; **Chy**, ceratohyal; **csl**, central sensory line; **d.end**, ductus endolymphaticus; **d.pr**, dorsal process; **d.sp**, dorsal spine; **f.bhy**, buccohypophysial foramen on parasphenoid; **fen** fenestra; **GPE**, direction of Greatest Principal Extension; **h.arch**, haemal arch; **h.sp.**, haemal spine; **Ign**, inferognathal;

IL, interolateral plate; **ioc**, infraorbital canal groove; **l.ind**, lateral indentation in parasphenoid; **llc**, main lateral line sensory canal groove; **MD**, median dorsal plate; **Mg**, marginal plate; **mp.PNu**, mesial process on paranuchal plate; **n.arch**, neural arch; **n.can.**, neural canal; **not.**, notochord; **Nu**, nuchal plate; **oa.AVL**, overlap area for AVL plate; **oa.Nu**, overlap area for nuchal plate; **Occ oss**, occipital ossification; **Ot**, otolith; **p.pao**, paraotic plate; **PDL**, posterior dorsolateral plate; **pect**, pectoral embayment (margin) of AVL plate; **pel.b**, basal plate of pelvic fin; **pel.d**, distal element of pelvic fin; **PMg**, posterior marginal plate; **PMV**, posterior median ventral plate; **PN**, postnasal plate; **pnpr**, postnuchal process of paranuchal plate; **PNu**, paranuchal plate; **ppl**, posterior pitline; **PrO**, preorbital plate; **Psp**, parasphenoid; **PtO**, postorbital plate; **Sgn ant**, anterior superognathal; **Sgn post**, posterior superognathal; **SMg**, submarginal; **soc**, supraorbital canal groove; **Sp**, spinal plate; **SPE**, direction of Shortest Principal Extension; **sub-h.sp.**, sub-haemal spine; **Syn**, synarcual; **vpl**, ventral pitline; **zyg.**, zygopophosis.

SYSTEMATIC PALAEOLOGY

Class PLACODERMI McCoy, 1848
Order PHYLLOLEPIDA Stensiö, 1934

Diagnosis

Placoderms with greatly enlarged nuchal plate, slightly wider than long, surrounded by five pairs of smaller bones – paranuchals, marginals, postorbitals, post nasals and preorbitals. Paranuchal plate with well-developed postnuchal process. Rostral, pineal and central plates absent from skull roof. Anterior and posterior superognathals; anterior superognathal large and wide, posterior superognathal very small; inferognathal long, narrow anteriorly, wider posteriorly. Trunk armour broad and dorsoventrally flattened; median dorsal plate lacks an inner keel; anterior dorsolateral plate with long, narrow exposed area; posterior dorsolateral plate reduced or absent; anterior lateral plate small, rhomboid; posterior lateral plate absent. Anterior ventrolateral plate short and broad, with ossification centre near posteromesial corner; posterior ventrolateral plate triangular, with ossification centre near anteromesial corner; both plates relatively flat with straight, non-overlapping mesial suture. Interolateral plate long, narrow, with denticulate postbranchial lamina; anterior median ventral plate short, broad, separating interlaterals; posterior median ventral plate(s) small, narrow,

variable in number (0-2). Dermal ornament consists of smooth, slightly undulating, subconcentric ridges, locally of rows of tubercles. Pelvic fins small; dorsal fin absent; caudal fin large, epicercal.

COWRALEPIS MCLACHLANI

new genus and species

Figs 1-20

‘a new genus and species of phyllolepid’: Krynen, 1998, 225.

‘a new phyllolepid’: Young, 1999, 144.

Name

The **genus** is named after Cowra (Aboriginal for ‘place of the rocks’), the nearest town in central west New South Wales; and *lepis* (Gk), ‘scale’.

The **species** name acknowledges the contribution of Mr Alex McLachlan, owner of ‘Mooroonbin’, near Cowra, NSW (which includes Merriganowry), in enclosing the quarry site and making it available to the Australian Museum for scientific investigation; also after the Lachlan River near where the first discoveries were made. Only one species, *Cowralepis mclachlani* sp. nov. is recognized at present from the Merriganowry site.

Repository

All of the described, figured and mentioned specimens in this paper are lodged in the palaeontology collections of the Australian Museum, Sydney, as indicated by the prefix **AMF**.

Holotype

AMF103767a, b, medium sized individual complete with tail, seen in dorsal and ventral view (Fig. 1A-D)

Figured material

AMF90003a (Fig. 4A, 6A); AMF90004 (Fig. 16C); AMF90007b (Figs 12A, 14A); AMF90011a, b (Figs 18E, F; Fig. 19); AMF90012 (Fig. 7H); AMF90018 (Fig. 5D); AMF90027 (Fig. 2C); AMF90029a (Fig. 7G); AMF90034a, b (Fig. 2D); AMF90044b (Fig. 2I); AMF90048a (Fig. 17A, B); AMF90048b (Figs 17C, D); AMF90051 (Fig. 5C); AMF90053 (Fig. 2B); AMF90054a, b (Fig. 7D, E); AMF96747a (Fig. 2G); AMF96750 (Fig. 2E); AMF96751a (Fig. 13A); AMF96755a, b (Fig. 13C); AMF96762 (Figs 4B, 6B, 7C); AMF96764 (Fig. 16A); AMF96765 (Fig. 16B); AMF96779 (Figs 7A, B, 10E, 12E); AMF96780 (Fig. 10F); AMF96781 (Fig. 9A, B); AMF96783 (Figs 9E-G, 12F); AMF96784 (Fig. 7F); AMF96785 (Fig. 13D,

E); AMF96786 (Fig. 10G, H); AMF100018 (Fig. 5D); AMF103753a, b (Figs 5A, B, 6C, D); AMF103754 (Fig. 7I); AMF103755 (Fig. 10A); AMF103756 (Fig. 2A); AMF103763 (Fig. 13B); AMF103768 (Fig. 9D); AMF103770 (Fig. 8C, D); AMF103776 (Fig. 14B); AMF103778a (Fig. 2J); AMF103784 (Fig. 2H); AMF103787 (Fig. 10D); AMF104154b (Figs 8A, B, 9C); AMF104155 (Fig. 10C); AMF104157a (Fig. 2F); AMF104160 (Fig. 8F); AMF104164 (Fig. 10B); AMF127151a (Fig. 18D); AMF127152 (Fig. 8E); AMF127154b (Fig. 18B); AMF127156 (Figs 11A, B, 12B-D); AMF127159 (Fig. 18A); AMF127162 (Fig. 8G).

Locality

All of the figured material comes from a small quarry, the type locality (and only known exposure) of the Merriganowry Shale Member. The quarry (GR642750 6373750) is on a small rise on the east side of the Cowra to Forbes road on Mooroonbin property, 1.5 km northwest of Merriganowry homestead and 20 km northwest of Cowra, New South Wales.

Diagnosis

Moderately large phyllolepid, reaching ca. 35 cm in length. Widest part of nuchal plate lies just posterior to centre of ossification; anterior nuchal margin more angular than in *Placolepis*, less angular than in *Austrophyllolepis* and *Phyllolepis*. Nuchal plate same length as or longer than median dorsal plate in juveniles; nuchal plate 20-60% longer than median dorsal plate in adults. Supraorbital canal, infraorbital canal and pit-line grooves not developed on nuchal plate. Lateral line canal groove on paranuchal plate diverges anteriorly from nuchal margin and canal groove crosses anterolateral margin between 78-92% PNu length. Marginal plate separates postorbital and paranuchal plates. Marginal plate and posterior division of postorbital plate lack contact with the nuchal plate in juveniles, leaving fenestra between them; marginal plate and posterior division of postorbital plate meet lateral margin of nuchal in adults, fenestra reduced. Posterior dorsolateral plate present; small, subtriangular, hidden under lateral margin of median dorsal plate; posterior lateral plate absent. Anterior and posterior median ventral plates both present. Occipital region of endocranium ossified; vertebral column fused anteriorly, forming long narrow synarcual under median dorsal plate.

Remarks

In addition to *Cowralepis* gen. nov. described here, there are now five other named genera of phyllolepid - *Phyllolepis*, *Austrophyllolepis*, *Placolepis*, plus two

new genera recently described by Young (in press) from the Middle Late Devonian of the Pambula area, southeastern New South Wales. The later are known only from a handful of dissociated, and mostly incomplete, head and trunk plates.

Cowralepis differs from all of these in that the head shield is longer than the trunk shield; it is also the only phyllolepid known in which a fenestra is developed between the nuchal (Nu) and lateral cranial plates (PtO, Mg, PNu). *Cowralepis* differs from *Phyllolepis*, *Austrophyllolepis* and *Placolepis* in the presence of a posterior dorsolateral plate (PDL) in the trunk shield; a feature it apparently shares with the two new genera from near Pambula, NSW (Young, in press) discussed below.

DESCRIPTION

The three main developmental divisions of the skull and skeleton in vertebrates are

- a) dermal skeleton - includes the skull roof, cheek and operculum, denticulated or tooth-bearing bones of the palate and inside and outside of the lower jaw, and small dental plates of the buccal cavity and inside visceral arches.
- b) endocranium.
- c) visceral skeleton - Meckel's cartilage plus palatoquadrate, forming the core of the upper and lower jaws, plus branchial arches.

Dermal skeleton

The **head shield** of phyllolepid consisted of a very large nuchal plate (Nu) bordered anteriorly and laterally by five pairs of smaller plates, interpreted here as the preorbitals (PrO), postnasals (PN), postorbitals (PtO), marginals (Mg) and paranuchals (PNu), the last of which articulate with the trunk shield. Another pair of small plates, the submarginals (SMg) flanked the Mg plates laterally, but were only loosely associated with them.

Nuchal

In *Cowralepis* the Nu was slightly wider than long and sub-polygonal in shape (Fig. 6A, C, 15A) with the greatest width posterior to the centre of ossification. In this it is closest to *Placolepis* and differs from *Phyllolepis* and *Austrophyllolepis*, in which the Nu is always widest anterior to the centre of ossification (Fig. 20B). The anterior margin of the Nu was more angular than in *Placolepis* and less angular than in *Phyllolepis* and *Austrophyllolepis*.

Cowralepis differs most noticeably from

Placolepis, *Austrophyllolepis* and *Phyllolepis* in the relative lengths of its nuchal and median dorsal plates. In the other three genera the Nu plate is always shorter than the MD. In all but a few *Cowralepis* specimens it is the Nu that is longer, sometimes much longer, than the MD. Eighty *Cowralepis* specimens were selected in which the dorsal shield was well preserved and the Nu and MD plates were closely associated and lying in line. Unlike length/breadth measurements, the relative lengths of such plates should be unaffected by the tectonic deformation.

The results, illustrated graphically in Fig. 3A, show the relative length of the Nu and MD plates in a wide range of growth stages of *Cowralepis* and appear to indicate a dramatic increase in length of the head shield relative to the trunk shield during ontogeny.

Length Nu+MD	sample number	Nu/MD x 100
30 – 50 mm	20 individuals	av. 110.7%
50 – 70 mm	33 individuals	av. 107.8%
70 – 90 mm	10 individuals	av. 108.8%
90 – 110 mm	11 individuals	av. 123.2
110 – 130 mm	2 individuals	av. 113.5%
130 – 150 mm	2 individuals	av. 134.0%
150 – 170 mm	2 individuals	av. 139.0%

In only a few specimens of *Cowralepis* was the Nu plate slightly shorter than the MD. In sixty-three individuals with a combined Nu + MD length between 30 mm and 90 mm, the Nu plate was on average 8–10% longer than the MD. The main increase in the relative length of the head shield appears to have taken place from 90 mm (Nu + MD) upwards, with many specimens known in which the Nu plate is 20–40% longer than the MD.

In the holotype, AMF103767 (Figs 1A, 3A), the Nu is 32% longer than the MD; in AMF90003A (Figs 4A, 6A) the Nu is 39% longer. The most spectacular example is also the largest known specimen of *Cowralepis*, AMF103754a (Fig. 7I) in which the Nu plate is 60% longer than the MD.

These results indicate that, in at least one phyllolepid, *Cowralepis*, the head shield grew relatively larger than the trunk shield during later stages of growth and the head shield/trunk shield length index was not fixed but varied with age.

Cowralepis differs from all other phyllolepid genera in that only one pair of sensory canal grooves cross onto the Nu plate from the surrounding circum-nuchal plates; this is the central sensory line (Figs 2, 5A, C, 15A; csl) which is also visible on the ventral surface of the Nu (Figs 4B, 9A, 11). In contrast, three pairs of sensory canal grooves cross onto the Nu plate in *Austrophyllolepis* and four pairs in *Placolepis* and

Phyllolepis (Fig. 20B), as discussed below.

Circum-nuchal plates

The two anterior pairs of plates on the head shield were interpreted differently in *Placolepis* Ritchie (1984, fig. 2) and *Austrophyllolepis* Long (1984, 264, fig. 1). The writer followed Denison (1978, fig. 29) in identifying the median pair as the postnasal plates (PN) flanked by preorbital plates (PrO) plates; Long interpreted the median pair as the PrO plates flanked by the PN plates. The general consensus now is that the latter version is preferred, with the qualification that some uncertainty remains about the homology of the plates identified as the postnasals (Fig. 15A).

Preorbital plate

The PrO plates that form most of the anterior margin of the head shield are subrectangular, wider than long, and meet mesially in a sinuous suture. They are subdivided longitudinally by the supraorbital sensory canal groove (Fig. 15, soc) into a smaller mesial portion and a larger lateral division. The anterior margin of the head shield in *Cowralepis* (Figs 1, 2, 4–6, 13A, 14B) is straighter than in *Placolepis* and *Austrophyllolepis* and was not indented medially as in *Phyllolepis* (Fig. 20B).

In *Cowralepis* the suborbital canal (soc) terminates at the posterior margin of the PrO plate and does not cross onto the nuchal plate as in *Placolepis*, *Austrophyllolepis*, and *Phyllolepis*, in all of which the soc crosses onto the Nu plate, maintains the same course and converges towards the centre of ossification of the Nu (Fig. 20B).

An unusually preserved specimen of *Cowralepis* (Fig. 14B, soc) reveals why the supraorbital canal grooves appear to terminate suddenly at the posterior dermal margin of the PrO plates. In this specimen, seen in dorsal view, the circum-nuchal plates are in place but the nuchal plate has been lost, exposing the normally hidden overlap areas of the PrO and PN plates. The supraorbital canal grooves on the left and right PrO plates converge posteriorly towards the posterior overlap area where they turn sharply towards the midline. Just before reaching the midline they again turn sharply posteriorly to resume their original course, but would have been hidden under the anterior margin of the Nu plate.

Postnasal plate

The postnasal plates flank the PrO plates laterally to form the anterolateral corners of the head shield. The PN plates are relatively larger in *Cowralepis* than in *Placolepis*, *Austrophyllolepis* and *Phyllolepis* (Fig. 20B). The V-shaped canal groove on the PN

plate is interpreted as a loop of the infraorbital canal (Fig. 15A, ioc). It is also visible as a prominent ridge on the visceral surface of the plate (Figs 1B, 4B, 5B, 9A, E, 10B, C, 11, 13A). In *Cowralepis* and *Austrophyllolepis* the infraorbital canal does not cross onto the nuchal plate, unlike in *Placolepis* and *Phyllolepis* (Fig. 20B).

Postorbital plate

The postorbital plate is relatively larger in *Cowralepis* than in *Placolepis*, *Austrophyllolepis* and *Phyllolepis*, especially its posterior division. The infraorbital sensory canal groove (Figs 15A, 20B, ioc) continues over the PtO onto the nuchal plate as the central sensory line (csl), as in the other three genera. In small to medium-sized specimens of *Cowralepis* the posterior division of the PtO is separated from the Nu plates by a crescentic fenestra (Fig. 2G, fen). In larger specimens (Figs 1A, 5A, 6A, 11, 15A, B) the posterior division of the PtO contacts the Nu margin along its full length (cf. below).

Marginal plate

The Mg plate in *Cowralepis* is a small, subtriangular plate, longer than wide, tapering posteriorly and with a transverse anterior margin. It was closer in shape to the Mg plate of *Austrophyllolepis* than that of *Placolepis* (Long 1984, fig. 2B). The Mg is often partly obscured by the plates around it (Figs 1A, 2, 5A, B, 6A, B) and its shape is most clearly seen in ventral views of the head shield (Figs 4B, 6B, 14A) or in specimens that are dissociated (Fig. 7F). A small projection on the mesial margin of the Mg fitted into a notch in the PNu plate where the lateral line canal groove crossed over (Fig. 7F).

The Mg separated, and was overlapped anteriorly and posteriorly by, the PtO and PNu plates (as in *Placolepis*). In smaller *Cowralepis* specimens (Fig. 2), the mesial margin of the Mg plate fell far short of the Nu margin, leaving a fenestra (shared with the PtO) between them. In larger individuals, the Mg plate enlarged mesially until it just met the nuchal margin, although it is not clear if an overlap relationship had developed between them.

In *Cowralepis*, the relationship between the Mg plate and the plates surrounding it (PNu, PtO and Nu) changes during growth and appears to represent a morphological condition intermediate between *Placolepis* and *Austrophyllolepis*, as discussed below.

Paranuchal plate

The posterolateral corner of the head shield in phyllolepid was formed by a rather large paranuchal

plate with a long, broad lateral division and a narrow, tapering, postnuchal process (pnpr) that extended mesially almost to the midline (Figs 1, 2, 3A, C, 6A, 15A, B). The shape and overlap areas of the PNu in *Cowralepis* are best seen in isolated examples (Fig. 7F, G) or where the nuchal plate has been dislodged (Fig. 14B).

The lateral division of the PNu was traversed by a long curving groove that housed the lateral line sensory canal (llc) and crossed the Mg/PNu boundary at different levels in different phyllolepid taxa. This character, used by Long (1984, fig. 2A, 266) to differentiate *Austrophyllolepis* from *Placolepis* and *Phyllolepis*, is one of the most useful characters in separating and diagnosing phyllolepid taxa.

The length of the PNu, measured from its posterior margin to where the lateral line intersects its lateral margin, is expressed as a percentage of the total PNu length (cf. Young in press b, fig. 2A). Because both of these dimensions lie in the same direction their ratios are not altered by tectonic deformation, unlike breadth/length ratios.

In *Austrophyllolepis* the lateral line canal crossed the lateral margin of the PNu at around 68-72% of total PNu length. It is thus intermediate between *Phyllolepis orvini* Heintz (1930) from Greenland (Stensiö 1934, pl. 5, figs 1, 2) in which the lateral canal crossed at 48-56% PNu length and *Placolepis* (Ritchie 1984, fig. 6A-C) where the canal crossed onto the Mg at the apex of the PNu, effectively 100%. In a new genus from southeastern NSW described by Young (in press b, figs 3A, C, 4A) the PNu llc index is 71%, placing it within the *Austrophyllolepis* range.

The same analysis was applied to the Merriganowry phyllolepid material. Thirty-six examples of *Cowralepis* PNu plates were measured, many of them representing left and right PNu plates from the same individual. In *Cowralepis* the lateral line groove crossed the PNu margin at between 78.5% and 92% of the PNu length, with an average of 86%. This range therefore falls intermediate between that of *Placolepis* and *Austrophyllolepis* but does not overlap with either of them.

The lateral line canal groove on the PNu plate of all phyllolepids turns sharply mesially towards the posterolateral corner of the nuchal plate. In *Placolepis*, *Austrophyllolepis* and *Phyllolepis* it continues onto the nuchal surface for a short distance as the posterior pit-line (ppl), but no trace of a pit-line has been detected in *Cowralepis*.

The mesial margin of the PNu plate (Fig. 7F, G) is formed by a well-developed overlap area for the nuchal plate (oa.Nu) and carries a short blunt process that lay under the posterolateral corner of

the nuchal plate. On the posterior margin of this process lies a deep groove directed anteromesially. It is suggested here that this groove (Fig. 7F, G, d.end) may have housed the endolymphatic duct that in most placoderms reached the surface via a small foramen on either the nuchal or paranuchal plate. In *Cowralepis* there is no visible surface opening on either plate but it is possible that the endolymphatic duct may have opened on the margin between the plates.

Gavin Young (pers.comm.) has recently described a new phyllolepid from the south coast of New South Wales in which the paranuchal plate bears a strongly developed mesial process on the inner margin of the PNu (Young in press b, figs 3A-C, 4A, B, mp.PNu) that would have projected under the corner of the nuchal plate. This mesial process is clearly comparable to, but much larger than, the small blunt process seen in *Cowralepis* paranuchal plates (Fig. 7F, G, mp.PNu).

Interrelationships of nuchal, paranuchal, postorbital and marginal plates.

The Nu, PNu, PtO and Mg plates in *Cowralepis* illustrate a condition morphologically intermediate between that in *Placolepis* and *Austrophyllolepis* (Figs 15A, 20B). They also document a remarkable change in the relationships of these plates throughout ontogeny.

Placolepis and *Phyllolepis* (Fig. 20B) illustrate the extremes of the range in the known phyllolepid genera. *Placolepis* differed significantly from *Phyllolepis* in the size and shape of its PNu plate (much shorter than in *Phyllolepis*) and in the relationships of the PNu with the Mg, PtO and Nu plates.

In *Placolepis* (Ritchie 1984, fig. 8E) the lateral line canal groove closely followed the PNu/Nu margin to the anterior corner of the PNu where it crossed over the Mg onto the PtO. The Mg plate in *Placolepis* thus separated the PNu and PtO plates and was overlapped mesially by the lateral margin of the Nu.

In *Phyllolepis* (Ritchie 1984, fig.8F) the lateral line canal groove on the PNu plate crossed from the much smaller Mg plate attached about midway along the PNu lateral margin. A large triangular anterior extension of the PNu (mesial to the lateral line canal) separated both the marginal plate and posterior part of the postorbital plate from any contact with the nuchal.

Austrophyllolepis (Long 1984, figs 2, 7, 10, 13, 19B) displayed a condition intermediate between that of *Placolepis* and *Phyllolepis*. The Mg plate was similar in size and shape to that of *Phyllolepis* but was attached more anteriorly to the PNu margin than in *Phyllolepis*. *Austrophyllolepis* also resembles *Phyllolepis*, but differs from *Placolepis*, in its large

anterior extension of the PNu (1984, fig. 2A), which separated the Mg and Nu plates and contacted the posterior mesial margin of the PtO (Long 1984, figs 2B, 19B).

The new evidence from *Cowralepis* complements that of *Placolepis*, *Austrophyllolepis* and *Phyllolepis*. *Cowralepis* resembled *Placolepis* in that the Mg plate separated the PtO and PNu plates, and the anterior division of the PNu did not contact the PtO. *Cowralepis* resembled *Austrophyllolepis* and *Phyllolepis* in that neither the Mg plate nor the posterior margin of the PtO plate contact the lateral margin of the Nu (leaving a fenestra between them) – but only in juveniles and smaller individuals (Fig. 2). In adult *Cowralepis* specimens the PtO meets the Nu along its full length while the Mg barely contacts the Nu, or just falls short, but it always separates the PtO and PNu plates (Fig. 15).

The distinctive shape of the nuchal plate in *Phyllolepis* appears to be the derived condition in phyllolepids, compared to that in *Placolepis*. It could have arisen by either:

- a) a posterior migration of the lateral line canal groove on the PNu plate - since the angle of the lateral canal on the PNu does not appear to have changed significantly in the different phyllolepid genera, nor have its relationships to the marginal and postorbital plates (Long 1984, fig. 2A; this paper Figs 15, 20B).
- b) OR, the alternative, preferred here, progressive enlargement of the anterior division of the PNu plate, mesial to the lateral line, first separating the Mg plate and, later, the posterior part of the PtO, from the Nu - i.e. that the distinctive, parallel-sided shape of the nuchal plate in later phyllolepids (*Phyllolepis*) is largely the result of differential anterior enlargement of the paranuchal plate mesial to the lateral line canal groove (Fig. 20B).

OR by a combination of both processes

Submarginal plate

One more dermal bone in the cheek area remains to be accounted for. Long described a small unornamented bone lying lateral to the marginal plate in *Austrophyllolepis*. It was only seen in two specimens, leaving its nature and identification uncertain. It lacked a laterosensory groove, appeared to be loosely attached to the cheek and was identified as the postmarginal plate (Long 1984, 284, fig.19B, C; PMg).

A similar, but much larger, plate is present in most of the articulated specimens of *Cowralepis* (Figs 1A,

2B, C, E-G, I, J, 4A, B, 5D, 6A, B, 7F, 14A, B, 19). Its size, shape and relationship to the Mg are best seen in AMF96784 (Fig. 7F). The plate was long, narrow and slightly curved, with a shallow convex dermal surface. A low ridge crossed its dermal surface obliquely from the posteromesial corner to the anterolateral corner. It lay against the lateral margin of the Mg, but was only loosely attached to it and easily dislodged. From its position lateral to the Mg this plate appears to have formed part of a moveable cheek or gill cover and must therefore be the submarginal plate (SMg), not the postmarginal.

A submarginal plate is present in many placoderms, loosely attached in the cheek area and usually closely associated with the hyomandibula (Janvier 1996 fig. 4.42.14). The long, narrow submarginal of the dorsoventrally flattened *Cowralepis* resembles that found in deep-bodied ptyctodonts such as *Ctenurella* (Moy-Thomas and Miles 1971, fig. 8.13; Miles and Young 1977, figs 15, 19; Long 1997, figs 25, 28, 29) and *Campbellodus* and *Austroptyctodus*, both from Gogo, W.A. (Long 1997, figs 5, 6 and 28, 29, 35 respectively) and there can be little doubt that they are homologous.

Trunk shield

The dorsal and ventral trunk armour of *Cowralepis* (Fig. 15A-C) is basically similar to that of other phyllolepid genera, with a few differences detailed below. The wide variation in length/breadth proportions of the trunk plates in *Cowralepis* (most of which can be attributed to regional tectonism) precludes the use of such measurements for diagnosis. The trunk (and cranial) plates of *Cowralepis* also display a wide variety of dermal ornament, ranging from almost smooth surfaces to dense subconcentric ridges, but whether this variation is inter-specific or intra-specific remains to be determined.

Dorsal trunk shield

The dorsal trunk shield of *Cowralepis* (Figs 1A, 2, 4A, 5A, C, 6A, D, 15A, B) consisted of a large, subpentagonal median dorsal plate (MD) flanked laterally by an extremely narrow anterior dorsolateral plate (ADL) carrying the lateral line canal groove. A broad anterior flange on the ADL fitted under the posterior margin of the PNu plate on the head shield. Supported laterally by a similar flange, the postbranchial lamina, on the adjacent anterior lateral plate (AL), this provided phyllolepids with a sliding neck joint like that present in actinolepids and wuttagoonaspids. The spinal plate (Sp), linking the dorsal and ventral shields laterally, was relatively small, with a short posterior spine.

The dermal surface of the **anterior dorsolateral plate** (ADL) was long and very narrow and often obscured by the adjacent AL and MD plates (Figs 1A, 5A, C). Much more informative are specimens of the ADL seen in ventral view and showing its full shape, including the extensive mesial and lateral overlap areas that contacted the ventral margins of the MD and AL plates respectively (Figs 7A, B, 13A, D, 15B).

In AMF96779 (Fig. 7A, B) numerous cranial and trunk plates from one individual had become dissociated before burial. They included ventral views of the left (Fig. 7A) and right (Fig. 7B) ADL plates; an otolith from the same individual is figured elsewhere (Fig. 12E). A strongly developed, smoothly rounded ridge (ant ridge) extends the full length of the ventral anterior margin of each ADL plate and presumably supported the anterior flange on the ADL that fitted under the PNu plate in the head shield to form the sliding neck joint.

The inner surface of both ADL plates display an unusual feature not previously recorded in phyllolepids. The course of the lateral line canal is visible as a narrow ridge (llc) on the inner surface, running the length of the plate. Where this meets the anterior margin another, more strongly developed, ridge emerges from the margin ventral to the lateral line canal ridge.

The second ridge diverges posteriorly from the lateral line canal at 20-25°, becomes broader distally and bifurcates near the rear margin. Along most of its length this inner ridge on the ADL plate would have underlain the AL plate, acting as a strengthening buttress (buttr AL) for the latter. The same features are also visible in two figured specimens of *Cowralepis* in which the ADL plate is preserved *in situ* (Fig. 13A, D).

No trace of either **posterior dorsolateral** (PDL) or **posterior lateral** (PL) plates has been reported in the dorsal shields of *Phyllolepis*, *Austrophyllolepis* and *Placolepis*, raising the question whether this was a primary or a secondary condition. Both PDL and PL plates are present in a wide range of arthrodires; separate PL plates are also found in early antiarchs and PDL plates in palaeacanthaspids and petalichthyids. This suggests that PL and PDL plates were primitive components of the placoderm trunk shield.

The presence of a rather large PDL plate has been deduced in two new phyllolepid genera from Pambula, NSW, described by Young (in press b), although the PDL itself has not been recovered in either. In one taxon the median dorsal plate displays a short straight posterolateral margin between the lateral and posterolateral corners (Young, in press b,

fig. 5A, B, lc, plc), interpreted as the attachment point for a PDL plate. In the second new taxon, the ventral posterolateral margin of the MD plate displays a long, narrow contact face for a PDL plate (figs 7B, H, 8B, cf. PDL). In both of these new genera the PDL plate probably extended well beyond the lateral margins of the MD.

Cowralepis provides another example of a phyllolepid retaining a PDL plate in its trunk armour and illustrates an interesting intermediate condition in the reduction and secondary loss of PDL plates from the trunk shield. PDL plates are preserved in many *Cowralepis* specimens at all stages of growth, including the holotype (Figs 1A, B, 4B, 5B, 6B, D, 16A, 19), but they are very unusual dermal plates in that they were not visible at the surface (Fig. 15A, B).

The explanation is simple: in *Cowralepis*, the PDL plate was reduced to a mere remnant tucked neatly under, and attached to, the lateral margin of the median dorsal and did not extend beyond it. This is best illustrated in AMF96762 (Figs 4B, 6B, 7C), seen in ventral view, where the right PDL is still in place but the left PDL had become detached and drifted sideways. This exposes a contact area for the PDL on the ventral side of the MD plate consisting of several shallow pits. The PDL was crescentic to sub-triangular, with a rounded and thickened lateral margin. The anterior extension of the PDL was still in contact with the posterior end of the ADL plate (Fig. 16A).

Ventral trunk shield

The ventral trunk shield (Figs 1B, 4B, 5B, D, 6B, D, 8F, 15C, 16A,B, 19) consisted mainly of a pair of large, wide, flat anterior ventrolateral (AVL) plates, bordered anteriorly by long, narrow interolateral (IL) plates, and posteriorly by a pair of smaller, subtriangular posterior ventrolateral (PVL) plates. Whether phyllolepids ever possessed, or have lost, paired anterior ventral (AV) plates, like those present in actinolepids, wuttagoonaspids and the Chinese petalichthyid *Eucaryaspis* (Liu 1991), remains unknown.

The **interolateral (IL)** plate was already known from *Phyllolepis orvini* (Stensiö 1936, fig. 21), *Phyllolepis woodwardi* Stensiö (1939, text-fig.2), *Austrophyllolepis* (Long 1984, figs 18, 20) and *Placolepis* (Ritchie 1984 fig. 11E-D). The IL in *Cowralepis mclachlani* is almost identical (Fig. 8 A-E), a long, narrow, slightly curved plate tapering mesially to a sharp point. The post-branchial lamina was strongly convex and ornamented with 9-10 parallel rows of very fine denticles (Fig. 8D).

Although an **anterior median ventral (AMV)** plate was reconstructed in *Phyllolepis orvini* (Stensiö 1969 figs 199A, B) the best evidence for an AMV in phyllolepids was provided by an articulated specimen of *Phyllolepis woodwardi* from Dura Den, Scotland (Stensiö 1934, text fig. 2D; 1936 text fig. 5; 1939 text fig. 2) in which a reasonably large, well-developed AMV is preserved *in situ*, flanked laterally by the interolateral plates (IL).

Long (1984) was unable to identify an AMV in the *Austrophyllolepis* material from Mt Howitt and omitted it from the reconstructions of *A. ritchiei* and *A. youngi* (1984, figs 7, 13). In several specimens of *Austrophyllolepis* (1984, figs 5, 6, 11D, 18C) the anteriomesial corners of the AVL are distinctly rounded and part of what may be a small AMV is visible in one specimen (fig. 18C). The writer also was unable to locate or identify an AMV plate in the dissociated material of *Placolepis* and omitted it from his reconstruction (Ritchie 1984, figs 2D, 8C), but again the anteromesial corners of the AVL plates are slightly rounded (figs 10J, K, 11F, G, 12A, B).

Cowralepis reveals that the apparent absence of an AMV plate in *Austrophyllolepis* and in *Placolepis* is most probably due to the vagaries of preservation rather than original absence. As noted above, well-developed and robust IL plates are present in several specimens of *Austrophyllolepis*, but all of them were slightly displaced. The AMV was a much smaller plate, easily dislodged and lost *post mortem*.

In many of the apparently complete, articulated specimens of *Cowralepis* from Merriganowry it is not uncommon to find both the AMV and IL plates missing. The explanation appears to be that, during burial and compaction of the wide but slightly convex, ventral trunk shield, the narrow, curved IL plates, which supported and presumably strengthened the anterior margin of the AVL plates, were displaced by flattening and swung forwards, especially in the midline, and were often lost. In the process, the associated AMV was also detached and, being much smaller, is easily overlooked.

Every stage of this process is illustrated by *Cowralepis*. Many specimens show the AMV and IL plates still *in situ* and in association (Figs 1B, 4B, 5B, D, 14A, 15C). In most of the specimens where the IL plates have sprung forward, the AMV is missing. Other specimens show the AMV almost in place but slightly detached (Figs 8A, B, E) and reveal its size, shape and overlap areas. The AMV was three times wider than long. Its anterior margin was slightly concave and the posterior margin was bluntly pointed medially, matching the rounded corners of the AVL plates against which it fitted. In AMF127152 (Fig. 8E)

the AMV displays two pairs of overlap areas; laterally to accommodate the sharp pointed mesial ends of the IL plates and posteriorly for the anteromesial corners of the AVL plates.

Rounded anteromesial corners are well displayed in most AVL plates of *Austrophyllolepis* (Long 1984, figs 4-7, 11-13) and are also present in AVL plates of *Placolepis budawangensis* Ritchie (1984, figs 10-12). On the new evidence from *Cowralepis mclachlani*, the writer would now have no hesitation in restoring an AMV plate in *Placolepis* even though none has yet been found. On balance it is suggested that most, if not all, phyllolepid probably retained an AMV plate in their ventral trunk armour.

The first evidence for a **posterior median ventral plate (PMV)** came from a specimen of *Phyllolepis woodwardi* from Dura Den, Scotland (Stensiö 1939, text-fig. 2) in which "fragments of bone, not nearer determinable" were noted and labelled (*px*) in the mid-ventral line at the junction of the AVL and PVL plates. Long (1984, 267) suggested that these may be ". . . fragments of the axial skeleton", exposed through a gap in the ventral trunk shield. He figured a rather large, narrow PMV plate in several specimens of *Austrophyllolepis* (1984, figs 7, 9B, 11D, 13, 18C) plus an example of ". . . an abnormal development" in a juvenile specimen of *Austrophyllolepis* displaying two PMV plates (figs 4C, 6).

The *Cowralepis* material indicates that this condition may not, in fact, be so abnormal in phyllolepid. In the holotype of *Cowralepis mclachlani* (AMF103767B, Fig. 1B) and in several other specimens (AMF127162, Fig. 8G) a single slender PMV is visible. More commonly two PMV plates are clearly present, the anterior PMV being normally longer than the posterior one (Figs 5D, 16B). But other specimens from Merriganowry with apparently intact ventral shield show no trace of a PMV at the intersection of the AVL and PVL plates (Figs 4B, 6B, 8F).

The new evidence from *Cowralepis* suggests that the number of PMV plates in phyllolepid was not fixed but could vary within a genus and, possibly, even within a species, from none to at least two.

Sensory canals on the trunk shield

The lateral line system continued posteriorly from the head shield over the narrow ADL plate on the dorsal trunk shield. In *Placolepis*, *Austrophyllolepis* and *Phyllolepis* an anterior mesial branch of this crossed onto the corner of the MD plate as the dorsal sensory canal groove (Long 1984, figs 7, 13; Ritchie 1984 fig. 2A, C) but no trace of this canal groove has been detected in *Cowralepis*.

In the ventral trunk shield, the only trace of sensory canal grooves consists of a short shallow stretch of the ventral pit line (*vpl*) parallel to the posterior margin of the AVL plate in a few specimens of *Cowralepis* in which the ornament is well developed (Figs 5B, 6D, 8F, *vpl*). The ventral pit line is also present in *Placolepis*, *Austrophyllolepis* and *Phyllolepis*.

Tooth plates and parasphenoid

Although lying deep inside the head, the tooth plates and parasphenoid originated as part of the dermal skeleton. Amongst the placoderms, only the arthrodires and the acanthothoracids had two pairs of gnathal plates in their upper jaw, the anterior and posterior superognathals (*Sgn*) that occluded against a single inferognathal plate (*Ign*) in the lower jaw. Where two pairs of superognathals are present the posterior pair are normally the larger.

The only previous evidence for tooth plates in phyllolepid comes from *Austrophyllolepis*, in which large, broad superognathals and narrower inferognathals were preserved in several specimens (Long 1984, figs 5, 6, 12C, 16, 17, 18B), although usually slightly displaced.

The upper and lower tooth plates are preserved in many specimens of *Cowralepis*, both *in situ* and in association (Figs 9, 10, 11, 14, 19) and have also been found as isolated elements. They confirm the presence of two pairs of supragathal elements in *Cowralepis*: a large anterior supragathal, corresponding closely to that of *Austrophyllolepis*, and a very small posterior supragathal, nestling against its posterolateral margin. The small posterior element has only been identified in about a dozen of the many hundreds of phyllolepid specimens from Merriganowry, and it is not surprising, given its size, that it was not located in the much smaller sample of phyllolepid specimens available from Mt Howitt.

The **anterior superognathals** (Figs 4B, 5B, 6B, D, 9A, E-G, 10A-C, G, H, 15C, D) were long, broad and flat, subtriangular in shape with a concave mesial margin. In the largest individuals of *Cowralepis* the anterior *Sgn* plates reached over 3 cm in length and 1 cm wide. They were broadest posteriorly and tapered anteromesially to a narrow apex near the anterior margin of the head shield where they met in the midline under the preorbital plates at an angle of 90-100° (Figs 14A, 19). The occlusal surface was densely covered with rows of small, sharp conical teeth radiating from the ossification centre of the plate and increasing in size towards the margins, but with a very sharp line of demarcation running up the midline towards the anterior apex (Fig. 10G, H); a similar linear feature can be seen in the superognathals of

Austrophyllolepis (Long 1984, figs 16, 18B).

The anterior Sgn in *Cowralepis* closely resembles the example depicted in *Austrophyllolepis ritchiei* (Long 1984, fig. 17), except that the teeth in the latter did not extend to the margins, leaving an edentulous rim all round the plate. The shape of this plate does not match that in the accompanying reconstruction (Long 1984, fig. 14B) where its posterior margin was shown as sharply truncated, straight and attached to a rounded plate.

In sharp contrast to the anterior plate, the **posterior superognathal** was minute, only 2-4 mm in diameter (Figs 9E-G, 10A, B, C). It was semicircular, with one straight or slightly concave margin. Because of its size it is often obscured by larger ventral plates in the fossil specimens. The original relationships of the three gnathal plates are best demonstrated in AMF96783 (Fig. 9E-G) where the inferognathal is in occlusion against the anterior superognathal and the curved margin of the posterior Sgn neatly fits into the posterior margin of the larger superognathal; its straight margin is therefore the posterior face. In three other examples (Fig. 10A-C) the posterior Sgn is completely exposed but slightly displaced.

Given the small size of this element, and the fact that in placoderms with two pairs of superognathals (arthrodires and acanthothoracids) the posterior element is normally larger than the anterior, Gavin Young (pers. comm.) has suggested another interpretation for this small plate in *Cowralepis*. Young et al. (2001, 673, fig. 5A, sc) noted a third small denticulate plate, also ca. 2mm across, at the posterior end of the posterior superognathal plate in a buchanosteid arthrodire from Taemas, NSW

The **inferognathal** (Ign) comprises two laminae meeting at right angles; a tooth-covered dorsal (horizontal) occlusal lamina and a smooth, vertical anterolateral lamina. In most *Cowralepis* specimens the Ign is preserved in occlusion against the anterior superognathal and shows only the smooth groove that housed Meckel's cartilage (Figs 9A, E-G, 10A, E, 11). The Ign was very narrow anteriorly, broadening out only in the posterior half; its occlusal area (Fig. 10D) was much smaller and narrower than that of the anterior Sgn and a row of larger teeth extended along the outer ridge to the anterior apex (not visible here because of the rotation) as in *Austrophyllolepis* (Long 1984, figs 16, 17). The posterior margin of the inferognathal was smooth, tooth-free and serrated or sharply pointed (Fig. 10D, E).

Parasphenoid

In many placoderms the palate bore a small bone, the parasphenoid, with a median foramen

for the buccohypophysial canal; whether this is the homologue of the parasphenoid in osteichthyan fishes is still uncertain.

The parasphenoid is well preserved *in situ* in many specimens of *Cowralepis* and was apparently firmly attached to the palatal surface of the endocranium. It is best displayed in specimens where the branchial ossifications are either not preserved or have been lost (Figs 5B, 6D, 8A, 9A-F, 10G, H, 15C).

Based on the new evidence from *Cowralepis*, the reconstruction of the subcranial ossifications of *Austrophyllolepis* (Long 1984, fig. 14A, B) needs to be modified. The parasphenoid is shown in the correct position but the superognathals lay farther forward, almost meeting under the anterior margin. The otoliths (which would have been covered by the parasphenoid in the position depicted) were situated more posterolaterally, lying between the parasphenoid and the paranuchal.

The *Cowralepis* parasphenoid was very large (up to 1/3 the length of the head shield), flat and thin and was centrally situated under the nuchal plate. Its overall shape is best displayed in AMF96781 (Fig. 9B), and it consisted of a slightly raised, lightly tuberculated central area which was widest posteriorly and tapered anteriorly. A single median buccohypophysial foramen (f.bhy) is situated level with the widest part of the plate.

The central raised area was surrounded by a wide, thin radiating flange with scalloped edges. It was deeply indented laterally (l.ind) opposite the buccohypophysial foramen as far as the central raised area and continues as a shallow tapering groove onto the central raised area. The *Cowralepis* parasphenoid does not differ significantly from that in *Austrophyllolepis* (Long 1984, fig. 17), known only from a few specimens.

In a review of parasphenoids in the Placodermi, Dennis-Bryan (1995) noted that parasphenoids had been recorded from 36 placoderm genera, of which all but three were arthrodires; one of the three exceptions was *Austrophyllolepis* (Long 1984). It was observed that placoderm parasphenoids appeared to be species specific, but were of limited use at higher taxonomic levels. In overall shape the *Cowralepis* parasphenoid most closely resembles those of the Gogo brachythoracid arthrodires, *Goujetosteus* and *Eastmanosteus* (Dennis-Bryan 1995, fig. 2 B, D), but these were much more robust structures and easily detached from the endocranium.

Placoderm parasphenoids were divided into two main types - 'primitive' and 'advanced'. 'Primitive' parasphenoids were flat, lacked lateral notches or grooves, had a central tuberculated area and a large

median buccohypophysial foramen, single or paired. 'Advanced' parasphenoids were thicker, with lateral notches and grooves and buccal foramina reduced; tubercles were reduced or absent, and a well-developed median ventral crest was developed.

In a prescient comment Dennis-Bryan (1995, 136) cited two notable exceptions, *Pholidosteus* and *Austrophyllolepis*; "The former is considered to be an advanced arthrodire but has the so-called primitive parasphenoid, and in the latter case the reverse is true. It is perhaps possible that the dorsoventrally flattened phyllolepis are more advanced among placoderms than was first thought."

Visceral skeleton

In many placoderms both the dermal skeleton and endocranium are known from a wealth of well-preserved material. The visceral skeleton of placoderms, however, is rarely preserved and is poorly known (Denison, 1978, 5-7; Janvier, 1996, 153). In most cases it was probably unossified and, even where perichondral ossification was present, it was often delicate and easily destroyed by taphonomic processes.

In all gnathostomes the principal paired visceral structures are the mandibular and hyoid arches and several branchial arches. The mandibular arch comprises the palatoquadrate and mandibular (Meckel's) cartilages, both of which may be perichondrally ossified and, in the hyoid arch, the main elements (when preserved) are the hyomandibula, ceratohyal and basihyal elements.

Prior to the discovery of *Cowralepis* the only direct evidence on the visceral skeleton in phyllolepis came from several *Austrophyllolepis* specimens in which various paired and unpaired ossifications were preserved lying against the ventral surface of the head shield, but displaced (Long 1984, figs 6, 16, 17, 18B, 20). Long based his interpretation (fig. 17) on the only example in which these ossifications appeared to be in association and reconstructed them as three pairs of bones plus a large median parasphenoid and a pair of otoliths (Long 1984, fig. 14A).

Long interpreted the three pairs of elements as the superognathals, metapterygoids (the middle division of the palatoquadrate) and the quadrates, and he reconstructed them as connected in series (Long 1984, fig. 14B). He also suggested (Long 1984, 281) that this series might only have developed at maturity. Many of the articulated *Cowralepis* specimens, juvenile and adult, show some or all of the same visceral ossifications (and many others) *in situ* and in association and reveal that Long's interpretation is invalid.

Quadrate or articular?

Immediately posterior to the gnathal plates, and in direct line with the inferognathal, lay a robust bone with a narrow posterior stem and a wide anterior margin. This bone was strongly perichondrally ossified but open at both ends (Figs 10F, 11, 12C, D, F). A prominent ventral ridge ran obliquely from its anteromesial to its posterolateral margin. Anterolaterally it flared out into a wide triangular flange, with a rounded anterior margin. Posteriorly, on the mesial side of the ventral ridge, there was a deep smooth-sided pit (Figs 10F, 12F).

Long interpreted this plate as the quadrate and reconstructed it as attached anteromesially to a large, flat plate which he labelled the metapterygoid (Long 1984, figs 14B, 17).

Cowralepis suggests a different interpretation. The same two plates are preserved in a large number of specimens, in place and closely associated (Figs 9A, E, F, 11, 14A). The robust bone (Long's 'quadrate') was not originally attached distally to the rounded plate (Long's 'metapterygoid') but lay lateral to it (Fig. 15C, D). Although they have sometimes drifted slightly apart *post mortem* they appear to have been closely associated throughout growth.

The anterior margins of both the rounded plate, and the robust plate lateral to it, covered (ie. lay below) the posterior ends of both the superognathals and the inferognathal. They therefore lay ventral to Meckel's cartilage. This would suggest that the latter cannot be the quadrate, as originally proposed, and it is interpreted here as the **articular**, the posterior ossification of the lower jaw.

Miles and Dennis (1979, fig. 11B-E) illustrated a small perichondrally ossified articular plate attached to the rear of the inferognathal in the brachythoracid *Harrytoombsia* from Gogo, Australia. More recently Johanson (2003, fig. 4) has figured large, well-ossified articular bones attached to the inferognathal in other Gogo brachythoracids (*Eastmanosteus*, *Gogopiscis* and *Incisoscutum*).

Metapterygoid or ceratohyal?

If the robust bone is the articular this raises the question – what was the rounded plate lying along its mesial margin? This was very thin and flat and normally seen in ventral view (Figs 9A, F, 11, 12C, 14A, 18F, 19, Chy) but occasionally in dorsal view (Fig. 14B, Chy). It consisted of two layers of perichondral bone separated by a thin sheet of cartilage and continued to grow throughout life, as indicated by the prominent semicircular growth lines on the flat plate, which radiate from a centre of ossification midway along the straight margin.

Since it lay ventral to the inferognathal (and to Meckel's cartilage) it cannot be the metapterygoid (a palatoquadrate ossification) as suggested by Long (1984) and it is interpreted here as the **ceratohyal** (Fig. 15C, Chy), a ventral element of the hyoid arch.

In smaller *Cowralepis* individuals (Figs 5B, 6D, 9A, E, F) the ceratohyal was slightly longer than the articular but fell a long way short of the midline. In larger individuals (Figs 11A, B, 14A) the ceratohyal was almost twice as long as the articular and had expanded anteromesially to make contact with, and fit neatly against, the concave lateral margins of a large robust median plate, discussed below.

Basihyal

Almost every *Cowralepis* specimen in which the gnathal, articular and ceratohyal elements are preserved also features a large, robust, median perichondral ossification lying anteromesial to the ceratohyals and a short distance posterior to the symphysis of the upper and lower tooth plates (Figs 1, 4B, 9A, B, E, F, 11, 14A, 18F). The distinctive features of this robust plate are illustrated here by stereopair images (Fig. 12A, B).

The plate is about three times as long as wide, with a flat basal platform, rounded anteriorly and posteriorly and with concave lateral margins. A prominent, narrow ventral keel runs most of the length of the plate. The keel is shallowest anteriorly where it divides over the basal platform into numerous radiating buttresses and rises gradually towards the posterior margin where it terminates in a deep pit that probably housed a ligament operating to lower the jaw. Midway along the basal platform, on either side of the keel, there is a small round pit with a raised rim, most clearly seen in AMF96783 (Fig. 9E,F; cf. also 12A).

In smaller individuals the ceratohyals are well-separated from this median plate (Figs 6D, 9A, F) but, during growth, they gradually increase in size until they meet the lateral margins of the median plate, extending almost to its anterior margin (Figs 11, 14A).

In virtually every specimen of *Cowralepis* in which it is preserved *in situ* this median bone lies posterior to, and is quite separate from, both the gnathal plates and the mandibular arch. The close lateral association with the ceratohyals confirms that it also lies ventral to the inferognathal and it is interpreted here as the anterior ossification of the hyoid arch, a median **basihyal**.

Long (1984, fig. 17) figured a rather shapeless, unnamed median bone in *Austrophyllepis* overlapping the anterior margin of the parasphenoid but this was not

identified or included in the reconstruction (fig. 14B). Given its close association with the parasphenoid this plate may be the homologue of the basihyal in *Cowralepis* (Figs 9A, B, 15C), but this can only be settled by the recovery of more phyllolepid material from Mt Howitt.

Basibranchials or hypobranchials?

In several medium-sized to large *Cowralepis* specimens in which the visceral skeleton is preserved, the large median plate interpreted above as the basihyal is closely followed posteriorly by up to four pairs of flat, rounded to irregular bony plates that meet in the midline (Figs 1B, 4B, 6D, 11, 14A, 18F, 19). The anterior pair sometimes even wrap around the rounded posterior margin of the basihyal (Fig. 14A). If the above interpretation of the mandibular and hyoid arch elements is correct, these four pairs of plates must be associated with the third to sixth visceral arches. This is very similar to Ørvig's reconstruction of the visceral skeleton in the ptyctodont, *Ctenurella* (Miles 1971, fig. 8.13).

Ossified basal visceral elements have only been recorded from *Pseudopetalichthys* (Stensiö 1969, Figs 168A, B), *Tapinosteus* and now in *Cowralepis*. Stensiö's reconstruction of the branchial skeleton in *Tapinosteus* (1963, figs 83A, B; 1969, fig. 166A, B), derived from serially sectioning the holotype, shows a median basihyal followed by three pairs of hypobranchials, (each pair subdivided with dotted lines) and depicted as separated by unpaired basibranchials. The reconstruction was based on a chondrichthyan model (e.g. *Chimaera monstrosa*; Stensiö 1969, fig. 169), consistent with Stensiö's proposed grouping of chondrichthyans, placoderms and acanthodians into his Elasmobranchiomorphi, an association no longer considered to be valid.

This raises the question – are the four pairs of visceral elements in *Cowralepis* the homologues of the basibranchials (which are median and unpaired in chondrichthyans) or the hypobranchials (which are paired)? Goodrich (1930) and others have suggested, from embryological evidence, that the basal visceral elements in gnathostomes may have been primitively paired. There is no trace of any median elements between the pairs of basal branchial elements in *Cowralepis* that met in the midline and the paired elements present here are interpreted as **hypobranchials** (Figs 6B, 11B, 14A, B, 15D, Hbr).

The whole complex of basal visceral ossifications under the head of *Cowralepis* (large disc-shaped ceratohyals, a robust basihyal and several pairs of hypobranchials) would appear to have provided a firm floor to the buccal cavity, and the deep pit on the

posterior face of the basihyal (Fig. 12B) may have housed a strong ligament that depressed the lower jaw.

There are many more specimens of *Cowralepis* displaying the visceral skeleton than those figured here and a fuller account, tracing its ontogenetic development, will be presented elsewhere.

'Suborbital'

Long (1984, figs 4A, 5, 14A, 16, 19) figured a small curved bone in the cheek area of *Austrophyllolepis* but found it difficult to homologise this with other placoderms because it lacked ornament and was folded into a ". . . double lamina with a large valley in between" (Long 1984, 283). The plate was interpreted as a greatly reduced and modified suborbital plate (SO) from its situation below, or lateral to, the PtO plate, just where the infraorbital sensory line of most placoderms divided to send a supraoral line ventrally.

A similar small curved bone is present in several specimens of *Cowralepis* (Figs 5B, 6D, 14B, 15C, hae), but is best preserved in AMF127156 (Fig. 11A, B), details of which are shown as stereopairs (Fig. 12C, D, hae). In this rather large individual of *Cowralepis* the bone is 6 mm long and 3 mm wide, bean-shaped and strongly convex. Its surface is very smooth and deeply creased longitudinally by a curving groove close to, and following, the concave margin.

In most of the *Cowralepis* specimens in which this element is present it does not lie near the lateral margin of the PtO (as depicted in *Austrophyllolepis*) but farther in, under the inner margin of the PtO plate and almost touching the posterior end of the bone interpreted above as the articular. The new evidence from *Cowralepis* does not support the earlier identification of this bone as a suborbital plate.

The very strongly convex shape, complete lack of ornament and its position rule out a dermal origin. Gavin Young (pers.comm.) has suggested it may be a small perichondral ossification of the visceral skeleton and, from its position near the mandibular joint, possibly a hyoid arch element, and this interpretation is provisionally accepted here (Fig. 15C, hae).

Endocranium

In many *Cowralepis* specimens two very robust, median ossifications lying entirely within the trunk armour are often clearly visible through the dorsal and ventral armour, which has been impressed onto them (Figs 4B, 6B). They are most clearly seen in situ in a few specimens where the ventral plates have either been lost, or are preserved as isolated elements (Fig. 13).

The shorter, wider, structure is the **occipital ossification**, the longer, narrower ossification is the **synarcual**, the anterior section of the axial skeleton (discussed below) and the junction between them is the craniothoracic articulation.

The **Occipital ossification** lies anterior to the neck joint and represents the ossified posterior (occipital) part of the endocranium (Fig. 13A, B, D, E; Occ oss). It does not include the otic region and extends from the anterior margin of the ventral trunk shield to the posterior margin of the head shield.

There is a discrepancy in shape between the occipital ossification in small individuals (Fig. 13D, E) and in larger specimens (Fig. 13A, B). In juveniles it is broad and flat, narrowest posteriorly with concave sides and a straight posterior margin (the neck joint). Anteriorly it flares into two round, flat processes meeting mesially, with a median notch on the anterior margin.

In larger individuals (Figs 4B, 6B, 13A, B) the occipital ossification is much longer, like two spools attached side by side. The lateral margins are still concave and the anterior margin is wider than the posterior margin, but the central shaft of each half of the ossification is smoothly rounded with one or more rows of regularly spaced deep pits, separated by narrow ridges, developed around the circumference at either end.

While this may indicate the presence of two species, differential development of the occipital ossification between small and large individuals, as noted here, has been described in pycnodontids by Miles and Young (1977, 166)

Otoliths and paraotic plates

Almost all articulated specimens of *Cowralepis* display two solid, bean-like structures lying against the ventral surface of the nuchal plate midway between the midline and the anterior process of the paranuchal plate (PNu). Long (1984, figs 6, 9, 11, 12, 17, 18C) identified similar structures in *Austrophyllolepis* as otoliths and the *Cowralepis* material supports this.

The otoliths were dense calcareous bodies, oriented anterolaterally (Figs 1B, 4B, 5B, D, 8A, 9A, 11A, B, 13D, 14B). They were very solid bodies, not hollow, as demonstrated by the fact that the nuchal plate has often been moulded over them, and they were proportionally larger in smaller individuals than in more mature ones. One specimen of an isolated otolith displays its aggregate crystalline nature and surface structure in fine detail (Fig. 12E)

In life, the otoliths were internal structures located within the fluid-filled sacculus of the left and right otic labyrinth and were deeply embedded within the

endocranium, the anterior part of which, in *Cowralepis*, was apparently cartilaginous. As noted by Long (1984, 281) the position of the otoliths in *Austrophyllolepis* (and now also in *Cowralepis*) corresponds closely to the site of the saccular cavities in *Buchanosteus* (Young 1979), *Kujdanowiaspis* (Stensiö 1963) and other euarthrodiere. Calcified otoliths have not been recorded from other placoderms, but their presence in both *Cowralepis* and *Austrophyllolepis* suggests that they were probably present in all phyllolepid. Otoliths were also present in the extinct acanthodians and are found in extant osteichthyans, but in both of these groups there are three separate otoliths in each otic capsule, not one.

The otoliths in *Cowralepis* display an interesting feature not observed in *Austrophyllolepis*. In smaller individuals the posterior half of each otolith is often overlain or, more correctly, underlain by a subcircular to irregular bony disc with concentric growth rings (Fig. 8B). In slightly larger individuals this disc had grown to cover two thirds of the otolith (Fig. 11A, B), and in the largest individuals it was large enough to completely cover the otolith, onto which it was moulded from below (Fig. 14A). Because these sub-otic plates appear to be underlain ventrally by the hypobranchial ossifications, and therefore lay dorsal to them, it is suggested that these plates were attached to the palate immediately under each otic capsule as paraotic plates (Fig. 15D, p.pao).

The nearest equivalent in placoderms appears to be a large pair of denticle-covered paraotic plates developed on the palate in *Nefudina qalibahensis*, a rhenanid placoderm from the Early Devonian of Saudi Arabia (Lelièvre et al. 1995, 111, pl.1, fig.1, p.pao). The paraotics lay immediately under the otic capsules and were attached to the palatal surface of a well-ossified endocranium, just posterior to a large denticulate parasphenoid. Their robust nature and denticulate surface suggests they may have been used in food processing. In contrast, the paraotics in *Cowralepis* were thin, smooth-surfaced discs, lacking ornament and may have served to protect the undersurface of the otic capsules. Gavin Young (pers. comm.) has suggested that they may represent areas of ossification on the floor of the endocranium.

Axial skeleton and fins

In many placoderms the anterior vertebral elements, housed within the trunk shield, were fused into a **synarcual** ossification on which rested the median dorsal plate. Stensiö reconstructed the posterior of the endocranium and a long narrow synarcual in *Paraleiosteus* (1969, fig. 34) in lateral view, and that of *Cowralepis* must have looked rather

similar.

The synarcual in *Cowralepis* was long and narrow and its overall shape is displayed in two individuals seen in ventral view, AMF96762 (Figs 4B, 6B) where it is overlain by the ventral trunk plates and AMF96751 (Fig. 13A) where the ventral plates have been lost, fully exposing both the synarcual and occipital ossifications. AMF96753 (Fig. 13C), an isolated synarcual, preserved in counterpart, displays both its dorsal (left) and ventral (right) surfaces revealing that, like the occipital ossification, it was clearly divided into left and right sections. The ventral surface displays a deep longitudinal median groove that widens anteriorly into an elongate diamond-shaped foramen.

Long's reconstruction of the trunk and fins in *Austrophyllolepis* (1984 Fig. 23), based on the few incomplete specimens available at the time (Long 1984, figs 21, 22), can be revised from *Cowralepis*. There is no evidence for the presence of a dorsal fin in *Cowralepis* (or in *Austrophyllolepis*), the pelvic fins were much smaller than shown and were tucked under the body close to the ventral shield, and the caudal fin was epicercal (= heterocercal) with the notochord/vertebral column supporting the upper lobe.

The vertebral column is fully known in only a few placoderm genera, the best examples of which are *Ctenurella* (Stensiö 1969, fig. 178) and *Cocosteus* (Miles and Westoll 1968, text fig. 48) in both of which a persistent unrestricted notochord was enclosed dorsally and ventrally by neural and haemal arches bifurcating around it.

Many specimens of *Cowralepis*, small and large, have the vertebral column and tail fin attached, often almost complete and preserved in part and counterpart in fine detail (Figs 1, 4, 16-18). Even the smallest specimens display the beginnings of a well-ossified backbone (Figs 2D, 18A). The complete exposure of the vertebral elements indicates that *Cowralepis* lacked any scale-covering, a feature also noted in *Austrophyllolepis* by Long (1984, 297).

In *Cowralepis*, the tail was relatively long and powerful, and the relative length of the dermal shield to the body and tail change during growth. In small to medium-sized individuals the body and tail forms 65-70% of the total length; in the largest specimens this drops to just over 50% of the total length (Fig. 16 B, C).

Cowralepis had at least 60 vertebrae posterior to the trunk shield and pelvic fin. Anteriorly these consist only of dorsal (neural) and ventral (haemal) arcualia but posteriorly they deepen to support the caudal fin and were supplemented ventrally by an additional row of sub-haemal elements (Fig. 18C,

sub-h.sp) extending to the tip of the sharply pointed tail.

The exquisite preservation of some *Cowralepis* specimens (Fig. 17A-D) allows reconstruction of the vertebral elements (Fig. 18C) and comparison with those of *Coccosteus* and with *Incisoscutum ritchiei* in which uncrushed vertebral elements were recovered by acid preparation (Dennis and Miles, 1981, 248-50, figs 21, 22).

In *Incisoscutum* the neural arch (housing the nerve cord) was separated from an overlying triangular opening (housing the dorsal ligament) by horizontal bony flanges that met mesially. In *Coccosteus* a similar transverse flange carried an anterior median bony projection that Miles and Westoll (1968, text. fig. 46) called the zygapophysis; by contrast, in *Incisoscutum*, the same flange carried a pair of well-developed zygapophyses.

The condition in *Cowralepis* was simpler; the neural arch was an open V-shaped incision with no transverse flange separating the nerve cord and dorsal ligament, and with a single prominent zygapophysis at the apex of the neural arch (Fig. 18C, zyg). The dorsal spines were long, narrow and angled sharply backwards.

Where the neural arch sat on the notochord it broadened out into large curved basal pads, as in *Incisoscutum* (Dennis and Miles 1981, fig 22). In the haemal arches the paired dorsal contact processes were oval with deep pits (Fig. 17D). The haemal spines were much longer than the dorsal spines and strongly sinuous in shape, especially in the caudal fin. An unusual feature in *Cowralepis*, not recorded in any other placoderm, was the development of an extra row of sub-haemal radial elements, considerably deepening the hypochordal lobe of the fin and increasing the propulsive force of the tail.

Pectoral fin

None of the remarkably complete *Cowralepis* specimens from Merriganowry display any trace of the pectoral fin which clearly lacked any scale covering, nor is there any trace of the scapulocoracoid or of fin basals, suggesting that these were probably cartilaginous and not perichondrally ossified. The size and shape of the pectoral fin in *Cowralepis* remains conjectural (Fig. 20A).

Pelvic girdle and fin

The pelvic girdle and fin skeleton is preserved in situ in many specimens of *Cowralepis*, of all sizes, including the holotype, AMF103767 (Figs 1A-D, 4B, 6B, 7H, I, 16A-C, pel.b, pel.d). It lay immediately behind, or slightly overlapped, the posterior margin of

the ventral shield but it has also been found detached and isolated (Fig. 7D, E).

The pelvic fin was first identified in *Austrophyllolepis*, based on two specimens (only one of which was figured) where it consisted of two perichondral ossifications, a larger anterior element, and a shorter, narrower, distal element (Long 1984, figs 21, 22, pel.b, pro).

Based on the many well-preserved specimens of the same element in *Cowralepis*, the anterior element (basal pelvic plate) preserved in *Austrophyllolepis* is probably incomplete. In *Cowralepis* the basal pelvic plate was longer and narrower, with slightly concave margins (Fig. 7D, E, H, pel.b). The left and right pelvic plates met in the mid-ventral line and diverged posterolaterally at about 45° to the body axis.

Long noted that part of the lateral margin of the basal plate appeared to bear "short grooves denoting serial divisions for articulation of cartilaginous pelvic fin ray elements" (1984, fig. 20, art; 285). No evidence of such grooves has been detected in *Cowralepis* and I suspect that this feature in *Austrophyllolepis* was probably an artefact of preservation.

The shorter distal element (Figs 4B, 6B, D, 7D, E, H, I, pel.d) was interpreted by Long as a propterygium (1984, figs 21, 22, pro), the anterior of three principal cartilages in the paired fins of elasmobranch fishes, and thus a pre-axial element. In contrast, the smaller bone in the *Cowralepis* pelvic fin is normally attached distally to the basal plate, and in line with it, unlike in *Austrophyllolepis* where it appears to have been displaced. This suggests that it was an axial element.

Janvier (1996, 244) noted that although one group of placoderms (ptyctodonts) may have possessed claspers on the pelvic fin, ". . . the problem with pelvic claspers is that they are apparently lacking in all other placoderms, although very few pelvic fins have actually been preserved. Long (1984) has described a peculiar club-shaped endoskeletal (probably metapterygial) element in the pelvic fin of the phyllolepid *Austrophyllolepis*; this may suggest the presence of a pterygopodium that supported the clasper."

The distal element of the pelvic fin in *Cowralepis* (Figs 1C, D; 6B, D; 7D, E, H, I; 16A, pel.d) is interpreted as the homologue of the metapterygium in the elasmobranch fin.

Sexual dimorphism

Long (1984, 275, 286) discussed the possibility that the 'propterygial' element in *Austrophyllolepis* may have been a clasping organ, rather than just an extension of the pelvic fin. Zangerl (1981) pointed out that ". . . the pelvic girdle of *Austrophyllolepis*

showed some resemblance to the male clasping organs of primitive chondrichthyans, particularly *Cobelodus*". Judgement was suspended because of insufficient material; the only two specimens of the *Austrophyllolepis* pelvic skeleton were similar, with no evidence of dimorphism to indicate male and female versions.

This can now be re-examined using the numerous examples of pelvic fins in *Cowralepis*. Because of the vagaries of preservation, and its relatively small size, the pelvic fin is not always visible even in individuals in which the body and tail is well preserved. However, where it is preserved, the pelvic fin skeleton is always approximately the same length in similar-sized individuals, with no evidence for larger and smaller variants, or for the presence of claspers, that might indicate sexual dimorphism.

Sexual dimorphism could still be present in the Merriganowry phyllolepid material, but it is difficult to see how evidence for it might be extracted from fossil specimens that have undergone strong tectonic deformation.

The cannibal from Cowra

If further confirmation was required concerning the topographic relationships of all the gnathal and visceral skeletal elements under the *Cowralepis* head shield it is provided by an unusual example of one individual that literally bit off more than it could chew!

AMF90011a, b is a moderately large *Cowralepis* specimen in which the vertebral column of a second, smaller *Cowralepis* is seen disappearing under the anterior margin of the head shield in the midline (Fig. 18E). That it is not just a case of accidental superposition of one fish on another is revealed by the counterpart showing the ventral surface (Fig. 18F) and by combining information from the part and counterpart (Fig. 19). In the larger individual most of the gnathal and branchial skeletal elements are present *in situ* and they even include the small left posterior superognathal (Sgn post.) exposed by separation of the articular from the ceratohyal.

The smaller fish skeleton is shown here in black (Fig. 19). The vertebrae continue posteriorly under the ventral margin of the head shield and over the right superognathal. They pass between the basihyal and the right ceratohyal into the buccal cavity where they terminate against the posterior margin of the ventral trunk plates of the smaller individual (PVL + AVL plates; shown in black), still in association. The size of the prey demonstrates that the mouth opening in *Cowralepis* was at least as wide as the anterior margin of the head shield.

The neural arches and their dorsal spines lie against the occlusal surface of the right superognathal and are overlain by the posterior part of the right inferognathal. Behind this the dorsal spines disappear under the anteromesial corner of the right ceratohyal that has been moulded over them. The vertebrae and associated trunk plates are partly overlain by several hypobranchial plates and the trunk plates disappear under the leading edge of the host's ventral shield (AVL plates); the left and right interolateral plates have swung forwards and the AMV is missing, as commonly occurs in phyllolepids.

This unique specimen confirms that the skeletal elements identified as basihyal, ceratohyals, articulars and hypobranchials, together with the inferognathals, all lay ventral to the palatoquadrate and superognathals.

An egg sac?

One of the most intriguing finds from Merriganowry, AMF127151, preserved in counterpart (but only as a natural mould) appears to be an egg sac (Fig. 18D). It is 3 cm long, 1 cm wide and contains perhaps 200 tightly packed, uniform, oval bodies, each 3-4 mm long and oriented parallel to, or slightly oblique to the long axis of the whole mass. The surface material of each oval body is finely granular. The well-defined margins suggest that these tightly packed oval bodies were originally enclosed in a membrane or sac. There is obviously no way to investigate what they once contained. The only animal remains recorded from Merriganowry are phyllolepid fishes, possible thelodont scales (in coprolites), and rare eurypterid fragments. It is at least possible that they represent unhatched fish eggs and are presented here for the record.

Relationships of phyllolepids

Since their first discovery in Scotland in the early 19th century (Agassiz 1844) the nature, origins and relationships of phyllolepids have been in dispute. At one time they were even thought to be ostracoderm agnathans (Woodward 1915, 1920) until Stensiö (1934, 1936, 1939) confirmed that they were rather aberrant placoderms.

Until the 1980s, phyllolepids were considered to be the sister group to the Arthrodira (Goujet 1984) and several workers have suggested a close relationship with a distinctive endemic Australian arthrodire, *Wuttagoonaspis* Ritchie, 1973 (cf. Janvier 1996, figs 4.44, 4.49). Phyllolepids and wuttagoonaspids, which have now been recorded over a wide area in Australia (Young and Goujet 2003), had a rather similar ridged ornament that has

been interpreted as a shared derived character of the two groups. In contrast, I (Ritchie 1973) suggested that phyllolepid and wuttagoonaspids were only distantly related, a view supported by Dupret (2004, 48) who does not consider the ornament ridges in phyllolepid and wuttagoonaspids to be homologous and proposes *Wuttagoonaspis* as a sister group to all other arthrodires. Goujet and Young (1995, fig. 2) and Goujet and Young (2004, fig. 1) included both the Phyllolepid and *Wuttagoonaspis* in the Arthrodira, but as a polytomy, leaving their interrelationships unresolved.

Dupret (2004) reviewed the phylogenetic relationships between actinolepids (which, like phyllolepid, had a sliding neck joint,) and other arthrodires, e.g. phlyctaeniids and brachythoracids (which had a rotating neck joint with articular condyles on the anterior dorsolateral plates). He grouped Phyllolepid with "Actinolepids" in "Actinolepidoidei", a paraphyletic assemblage, and suggested that Phyllolepid are the sister group to the Phlyctaenioidei (Phlyctaenii plus Brachythoraci).

Palaeogeographic distribution of phyllolepid

Of the ca 300 placoderm genera and eight placoderm orders that dominated the Devonian lakes, rivers and seas (Carr 1995), the phyllolepid display perhaps the most unusual stratigraphic distribution. In the former supercontinent of Laurussia (=Euramerica), where they were first found, phyllolepid are known only from the latest Devonian (Famennian). They are the only placoderm group with no Early or Middle Devonian fossil record in the Northern Hemisphere.

Fossil discoveries from Gondwana since the early 1980s provide a possible explanation for the sudden appearance of phyllolepid in the Northern Hemisphere and a solution to the mystery of their origins (Young 1986, 1987, 1990, 1993a, 1993b, 2003, in press a, b). With the exception of Venezuela and Antarctica, most of the phyllolepid finds from Gondwana have come from Australia, from much older deposits - Late Middle Devonian (Givetian) to Early Late Devonian (Frasnian) - than those in the Northern Hemisphere. They are also usually found, like their northern relatives, in freshwater sediments.

This disjunct distribution of phyllolepid, in time and space, provides strong support for a dispersal episode in the mid-Late Devonian (Frasnian-Famennian boundary) at which time northern Gondwana and Laurussia came close enough to each other to allow the exchange of predominantly freshwater fish faunas. Phyllolepid fishes survived in Laurussia until the end of the Devonian but have left no record in Asia.

It is clear that much more remains to be uncovered about the early history of phyllolepid placoderms and that Gondwana, and especially Australia, displays the greatest potential for discoveries illustrating the origins and radiation of the Phyllolepid.

Cowralepis mclachlani gen. et sp. nov. makes a major contribution to our knowledge of the Phyllolepid. The Merriganowry site in central west New South Wales provides an ideal base for a long-term, multi-disciplinary scientific research programme into the palaeontological, palaeoecological and sedimentological history of a Late Middle Devonian lake and its fauna covering tens, or hundreds, of thousands of years. Under proper scientific supervision, this can be combined with, and financially supported by, a unique, hands-on, educational facility and eco-tourism experience, with long-term economic benefits for rural New South Wales.

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The discovery of the Merriganowry site owes much to the late Mr Reg Dumbrell of Canowindra who discovered the remains of phyllolepid fossil fish near the Lachlan River and reported this to the Australian Museum.

The remarkable assemblage of fossil specimens illustrated here represents only part of the material excavated from Merriganowry between 1993 and 2004 by many hundreds of paying volunteers, supervised by myself and Dr Zerina Johanson from the Australian Museum. These groups have been organised by Ms Monica Yeung of Canberra and Mr Bruce Loomes of Canowindra, through Gondwana Dreaming Inc. of Canberra. My deepest thanks to them and to all the dig participants who (mostly willingly) relinquished their fossil finds to the Australian Museum for this project and whose financial contributions helped to fund our research.

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A NEW GENUS OF DEVONIAN PLACODERMS

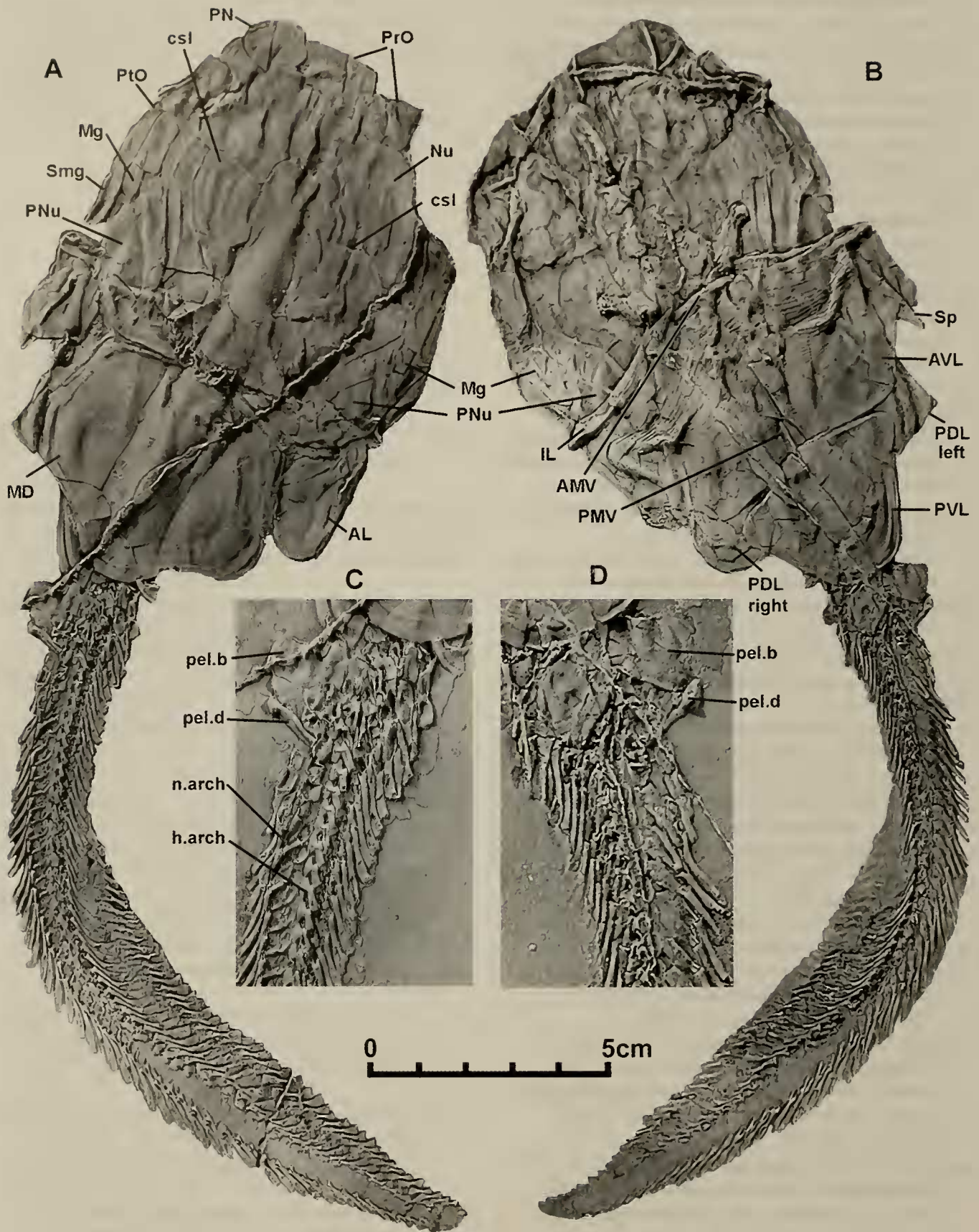


Figure 1A-D. *Cowralepis mclachlani* n. gen. and sp. AMF103767a, b. holotype, complete individual in part and counterpart. A) dorsal view; B) ventral view, C-D) detail, pelvic fins and vertebrae, in dorsal and ventral view respectively. Latex casts whitened with ammonium chloride sublimate.

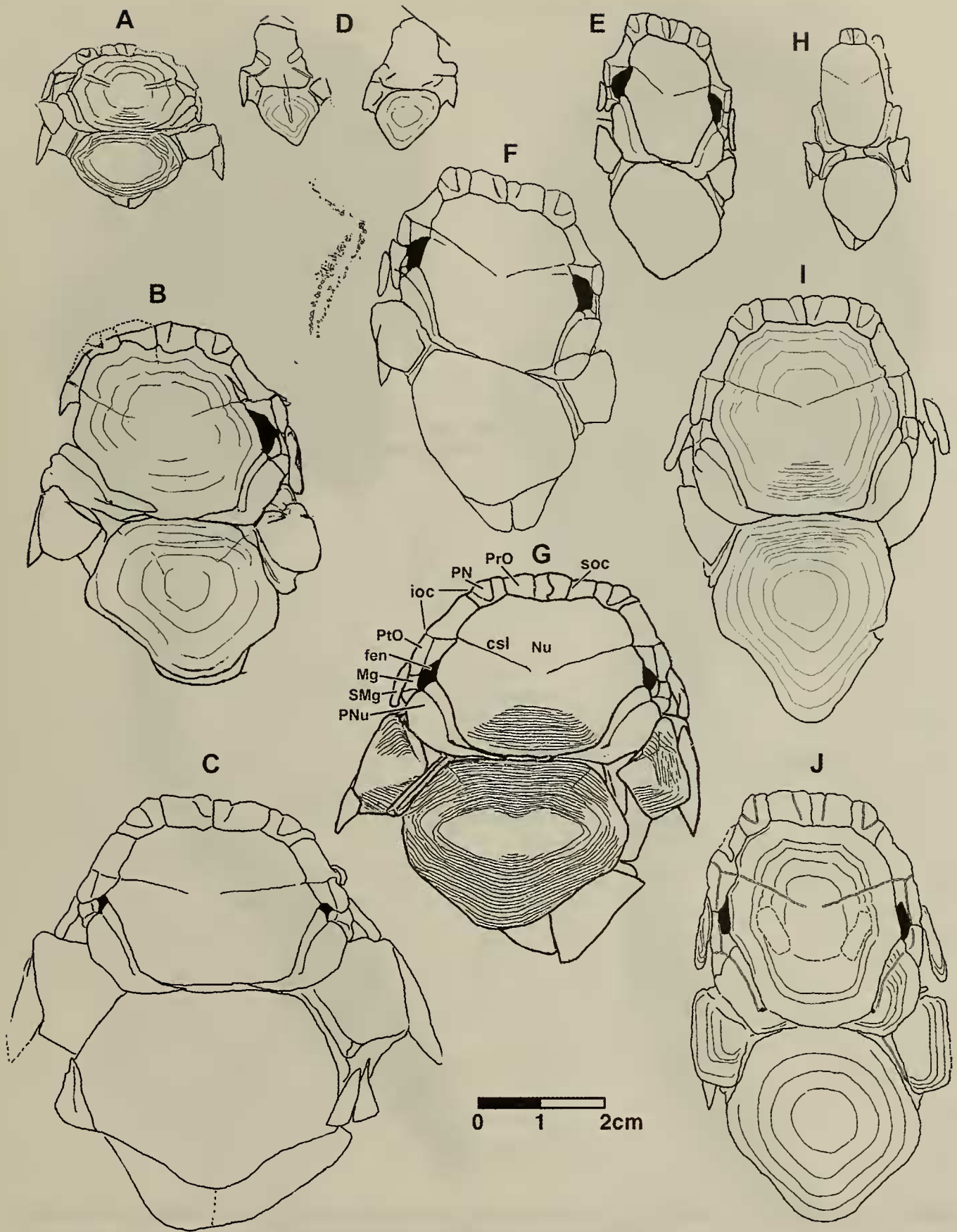


Figure 2A-J. *Cowralepis mclachlani* n. gen. and sp. Small to medium-sized individuals to the same scale illustrating the range of deformation in *Cowralepis* specimens from Merriganowry. A-C), short, broad symmetrical specimens; D-G) skewed specimens; (H-J) long, narrow symmetrical specimens. A) AMF103756; B) AMF90053; C) AMF90027; D) AMF90034a, b; E) AMF96750; F) AMF104157a; G) AMF96747a; H) AMF103784; I) AMF90044b; J) AMF103778a

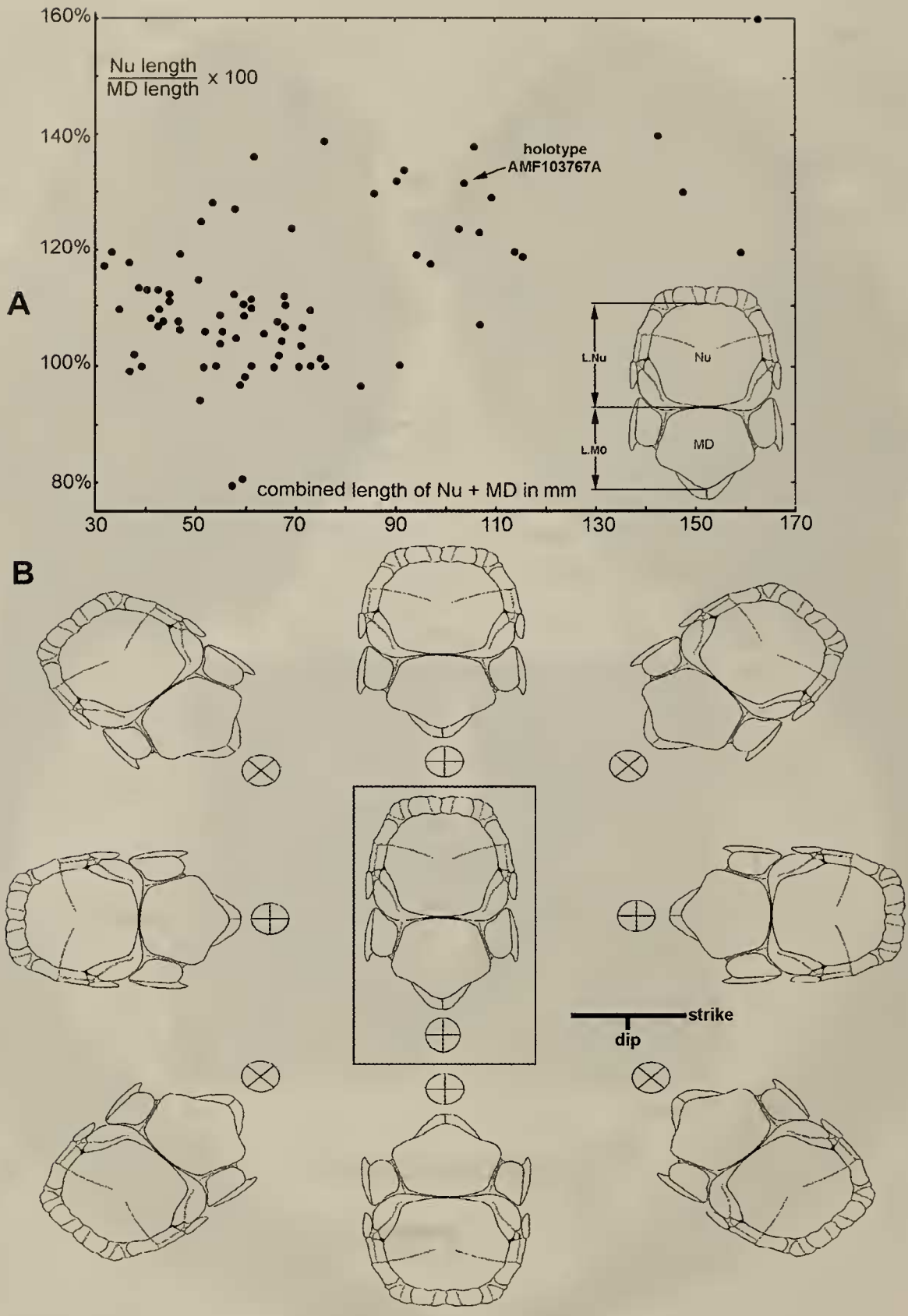


Figure 3A, B *Cowralepis mclachlani* n. gen. and sp. Tectonic deformation. A) relative lengths of dorsal plates in eighty *Cowralepis* specimens. Horizontal axis shows combined length of Nu+MD; vertical axis shows Nu/MD x 100. B) All *Cowralepis* specimens from Merriganowry have been tectonically deformed. The central figure depicts a hypothetical undeformed individual of *Cowralepis*. Surrounding figures, in different orientations, were enlarged by 10% in the direction of largest principal extension (GPE) and reduced by 10% in the direction of smallest principal extension (SPE), as indicated by accompanying strain ellipses. The strike and dip at Merriganowry are in register with the GPE and SPE of the strain ellipse, but this is probably coincidental.

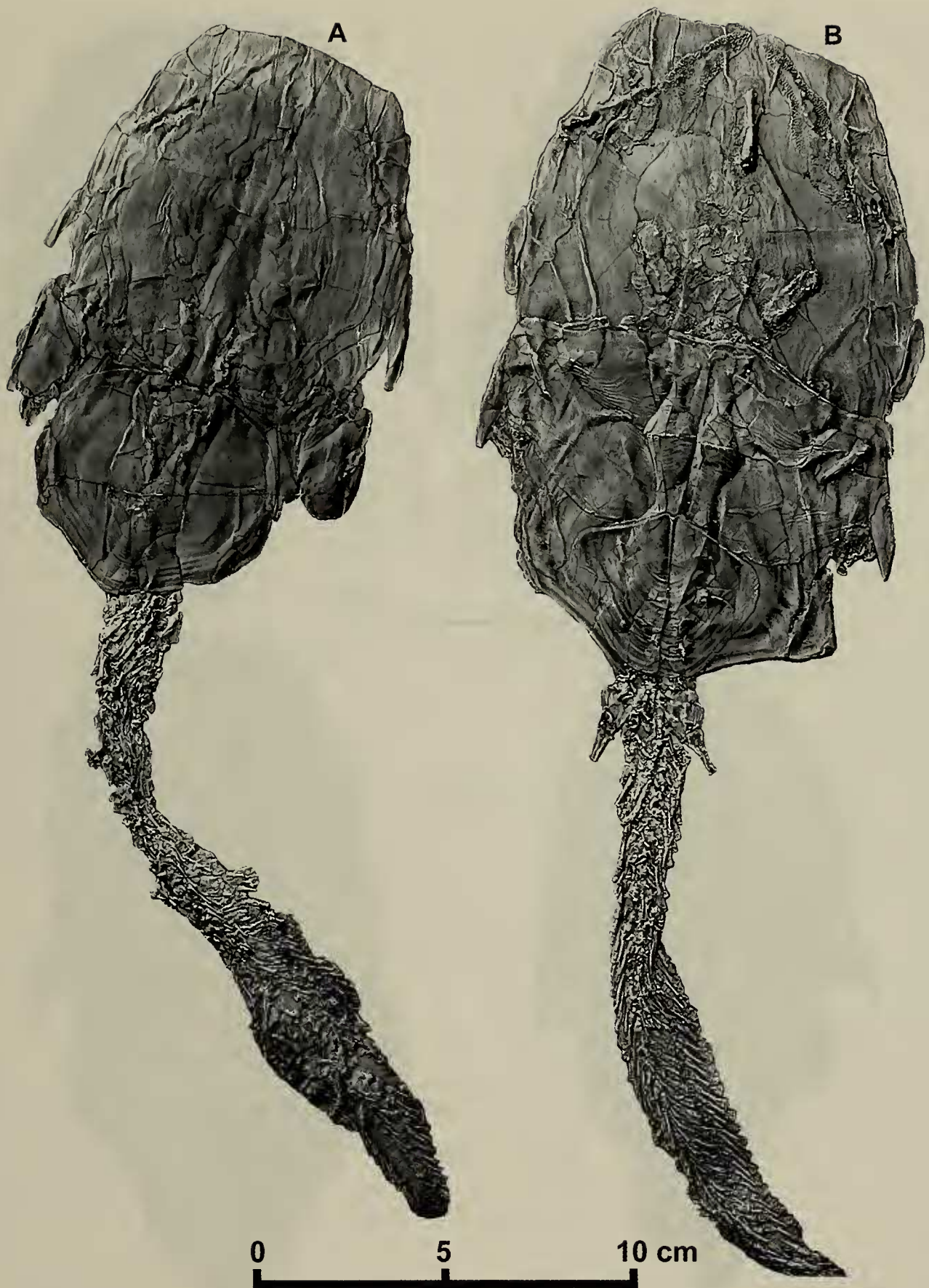


Figure 4A, B. *Cowralepis mclachlani* n. gen. and sp. Two large individuals with tail. A) AMF90003a, dorsal view; B) AMF96762, ventral view (cf. Fig. 6 for digitally modified versions of both). Latex casts whitened with ammonium chloride sublimate.

A NEW GENUS OF DEVONIAN PLACODERMS

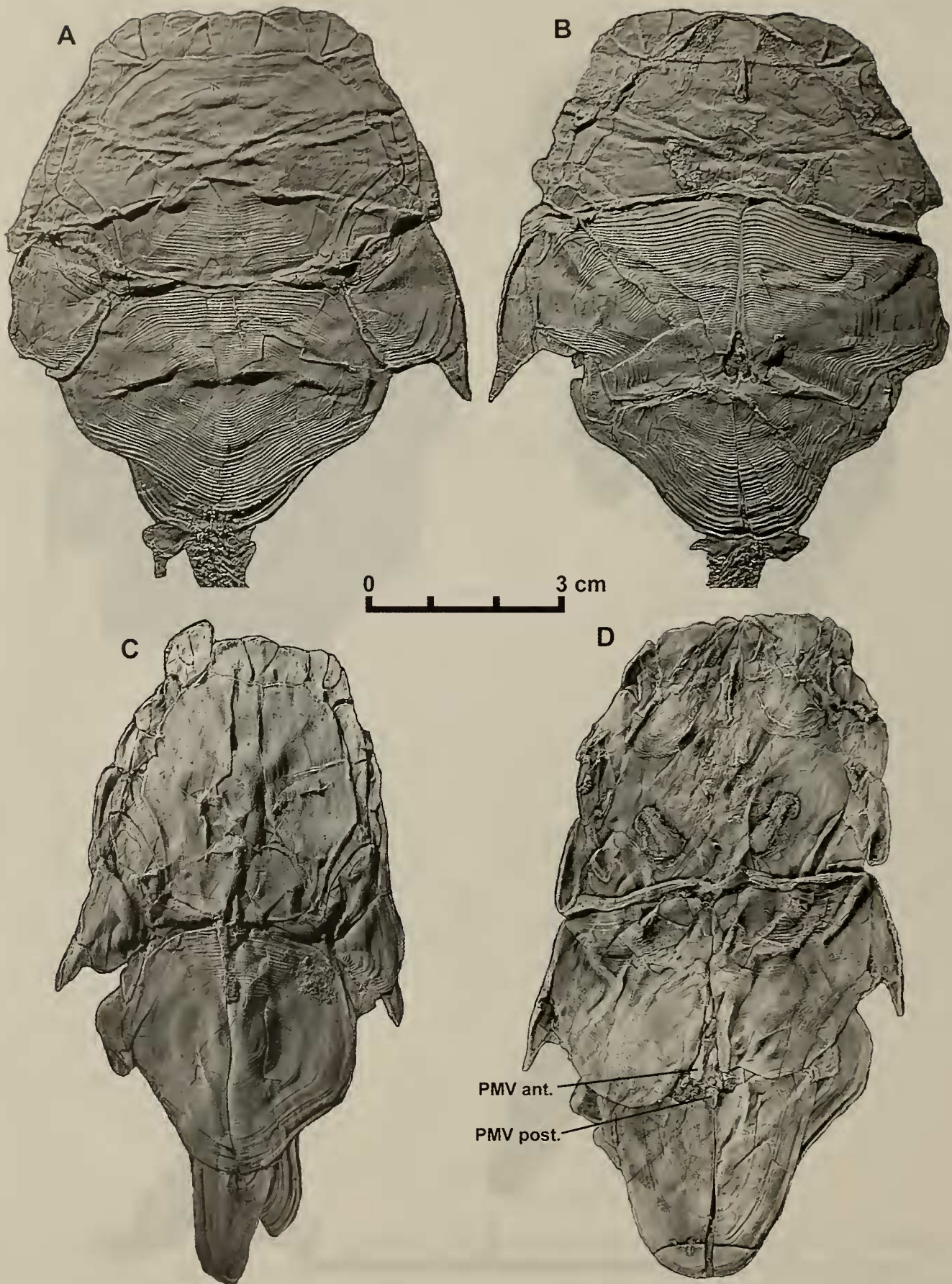


Figure 5A-D. *Cowralepis mclachlani* n. gen. and sp. Three symmetrical individuals illustrating short/broad and long/narrow examples of tectonic deformation. A, B) AMF103753a, b, dorsal and ventral (cf. Fig. 6C, D for same specimen after digital modification); C) AMF90051 dorsal view; D) AMF100018, ventral view. Latex casts whitened with ammonium chloride sublimate.

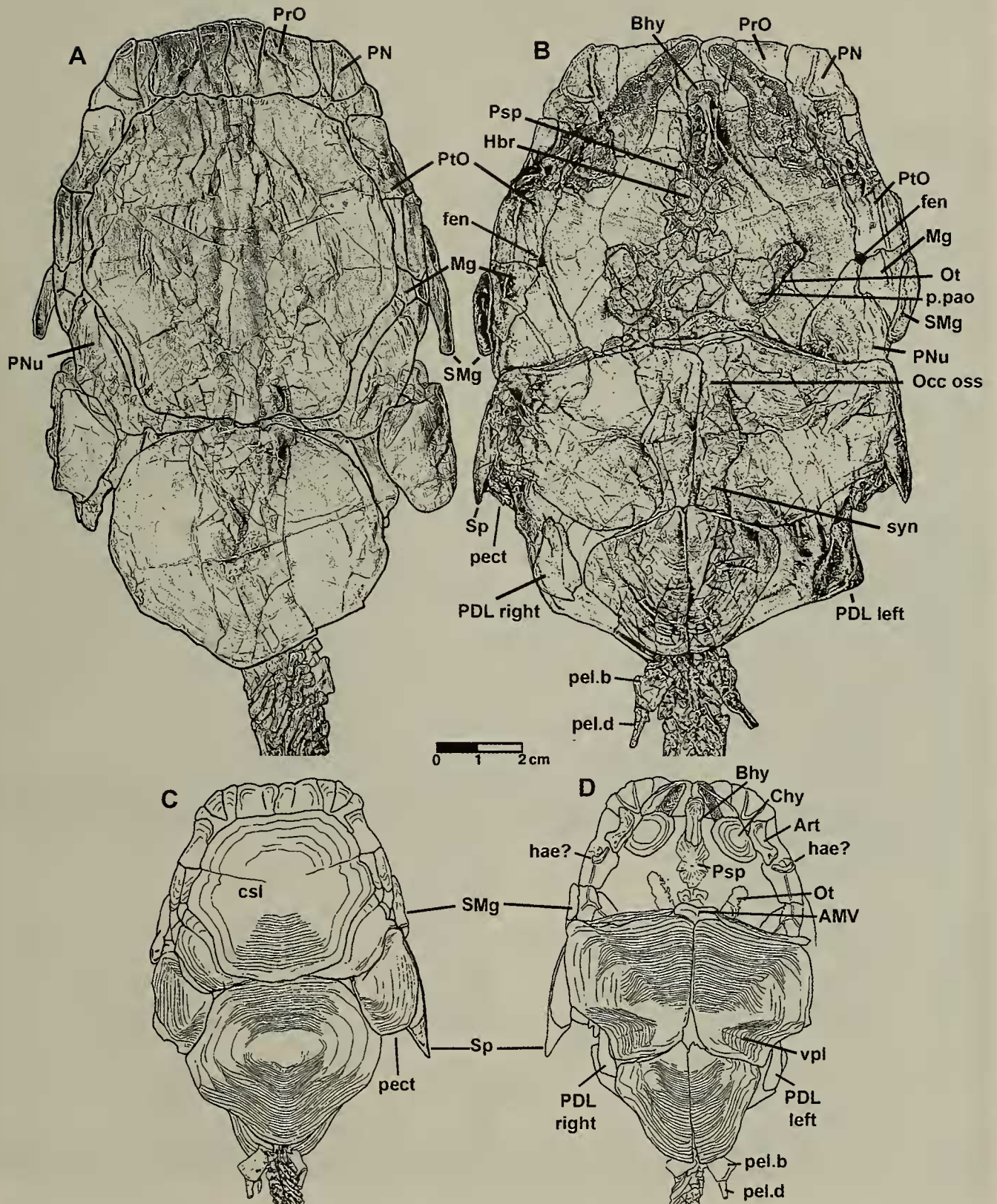


Figure 6A-D. *Cowralepis mclachlani* n. gen. and sp. Digitally modified versions of A,B) long/narrow and C,D) short/broad *Cowralepis* specimens restored approximately to original proportions. A) AMF.90003a, dorsal surface (cf. Fig. 4A); B) AMF96762, ventral surface (cf. Fig. 4B); AMF103753, dorsal and ventral views (cf. Fig. 5A, B).

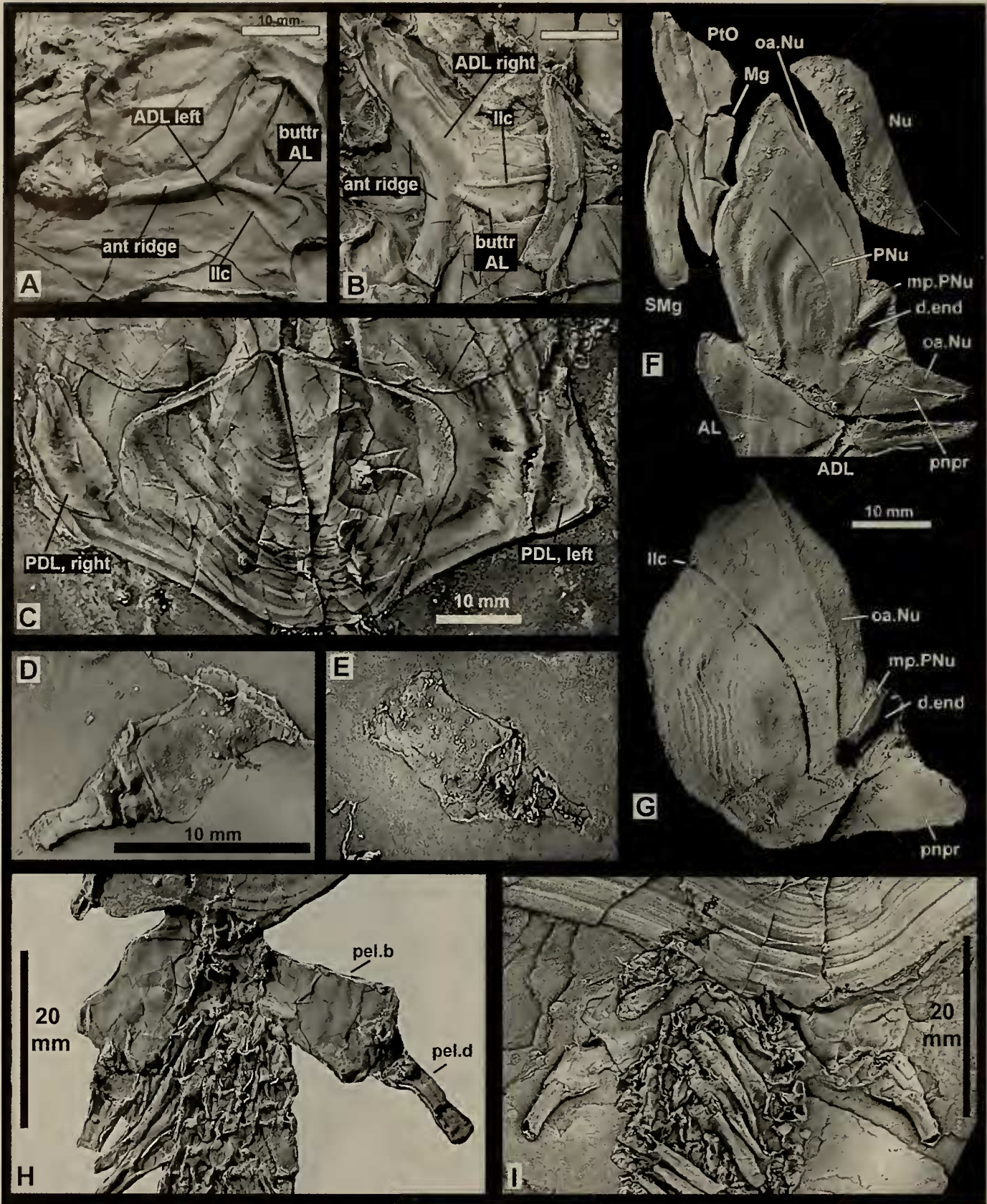


Figure 7A-I. *Cowralepis mclachlani* n. gen. and sp. A, B) AMF96779, left and right ADLs from same individual, in ventral view; C) AMF96762, left and right PDLs (cf. Figs 4B, 6B); D, E) AMF90054a, b, isolated pelvic fin skeleton, in counterpart; F) AMF96784, PNU with associated Mg, PMg and part of PtO, dermal view; G) AMF90029a, right paranuchal, dermal view; H) AMF90012, pelvic fins, dorsal view; I) AMF 103754, pelvic fins, dorsal view. Latex casts whitened with ammonium chloride sublimate.

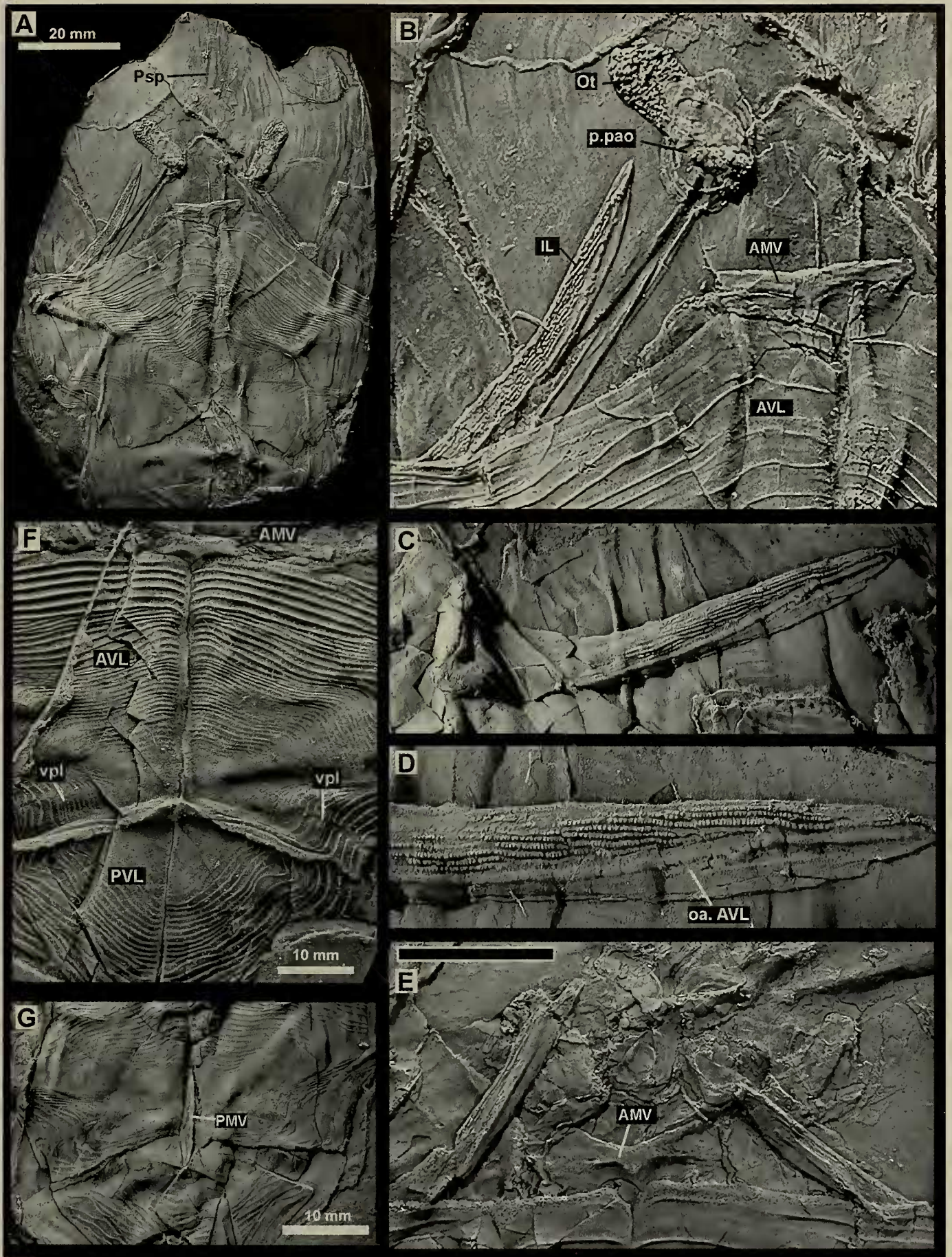


Figure 8A-G. *Cowralepis mclachlani* n. gen. and sp. Ventral trunk plates. A) AMF104154, partial head and trunk, ventral view; B) IL, AMV and otolith; C) AMF103770, right IL; D) detail of ornament; E) AMF127152, anterior ventral margin with AMV and both IL plates slightly dislodged; F) AMF104160, AVL and PVL plates; no PMV visible; G) AMF127162, AVL and PVL plates; one PMV present. Latex casts whitened with ammonium chloride sublimate.

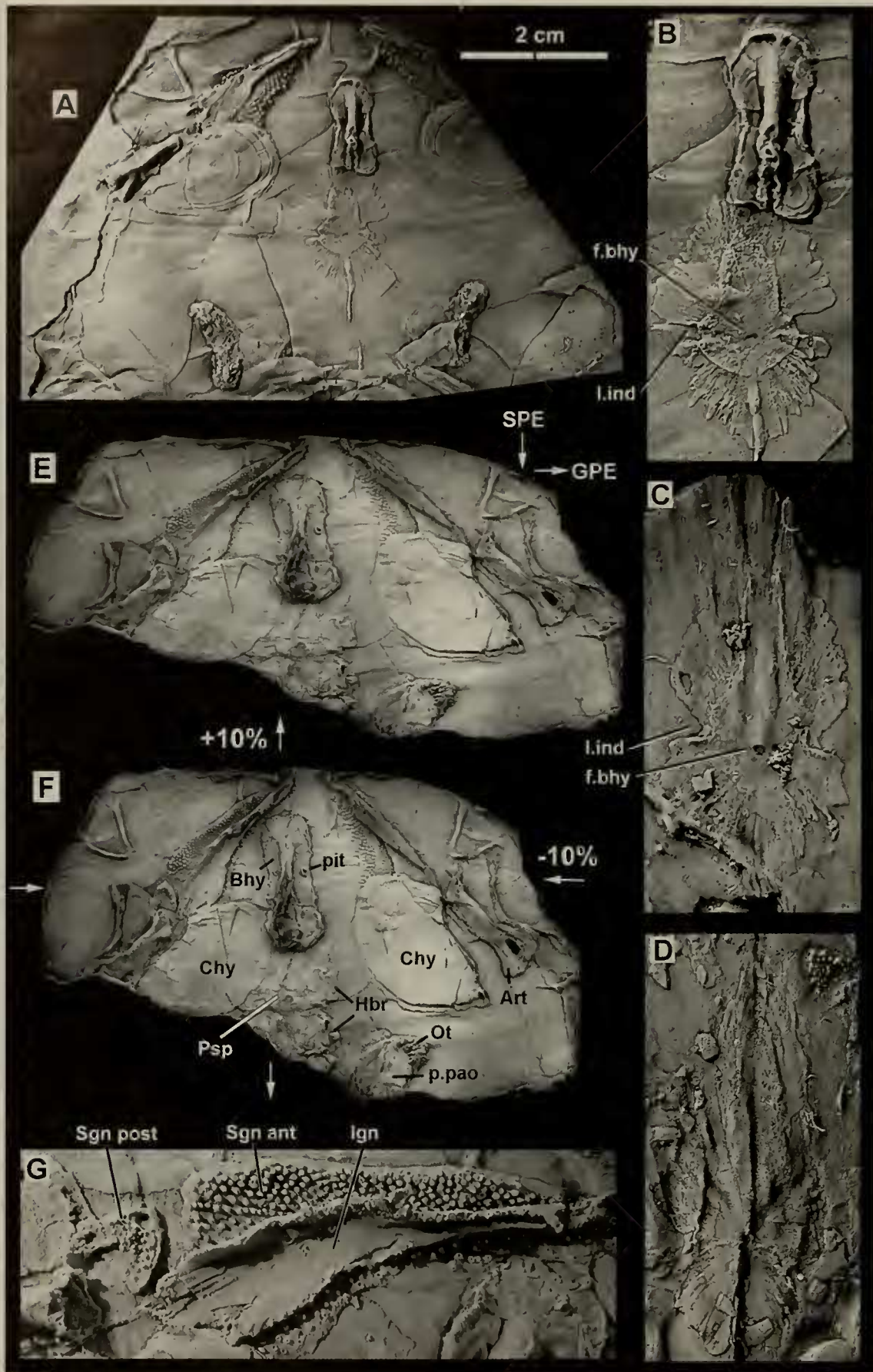


Figure 9A-G. *Cowralepis mclachlani* n. gen. and sp. A) AMF96781, ventral view; and B) AMF96781, detail of A); C) AMF104154, parasphenoid, ventral surface (cf. Fig. 8A); D) AMF103768, parasphenoid, dorsal surface; E) AMF96783, before digital modification; GPE and SPE indicate directions of Greatest and Shortest Principal Extension; F) AMF96783, after digital modification; arrows indicate direction and % of correction applied; G) AMF96783, right inferognathal and both superognathals in association. Latex casts whitened with ammonium chloride sublimate.

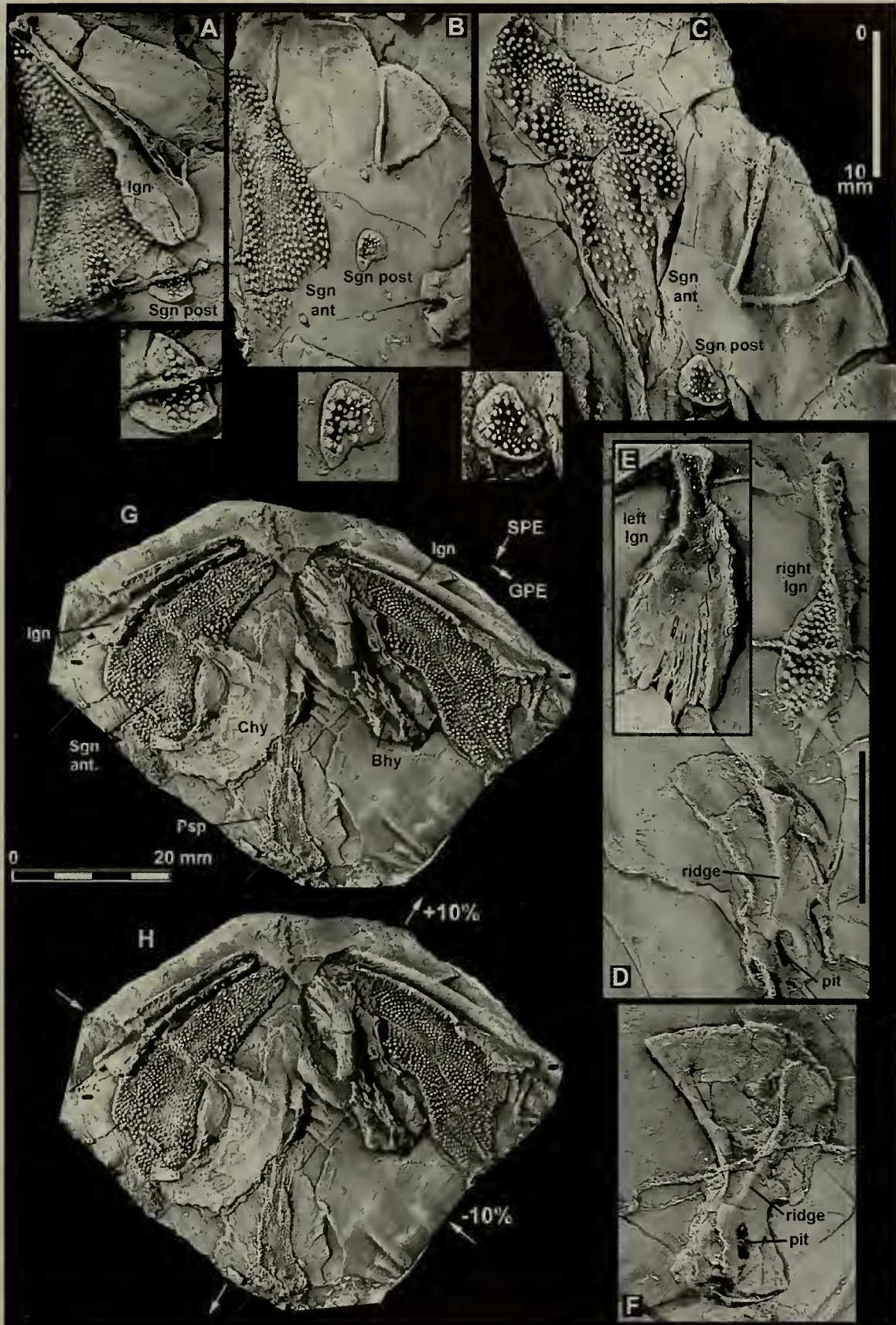


Figure 10A-G. *Cowralepis mclachlani* n. gen. and sp. Gnathal elements. A) AMF103755, left superognathals and inferognathal; B) AMF104164, left superognathals, inferognathal lost; C) AMF104155, left superognathals, inferognathal lost; D) AMF103787, right inferognathal and articular, lgn rotated to show occlusal surface; E) AMF96779, left inferognathal, ventral view; F) AMF96780, right articular, ventral view; G) AMF96786, before digital modification; GPE and SPE indicate directions of Greatest and Shortest Principal Extension; H) AMF96786, after digital modification; arrows indicate direction and % of correction applied. Latex casts whitened with ammonium chloride sublimate.

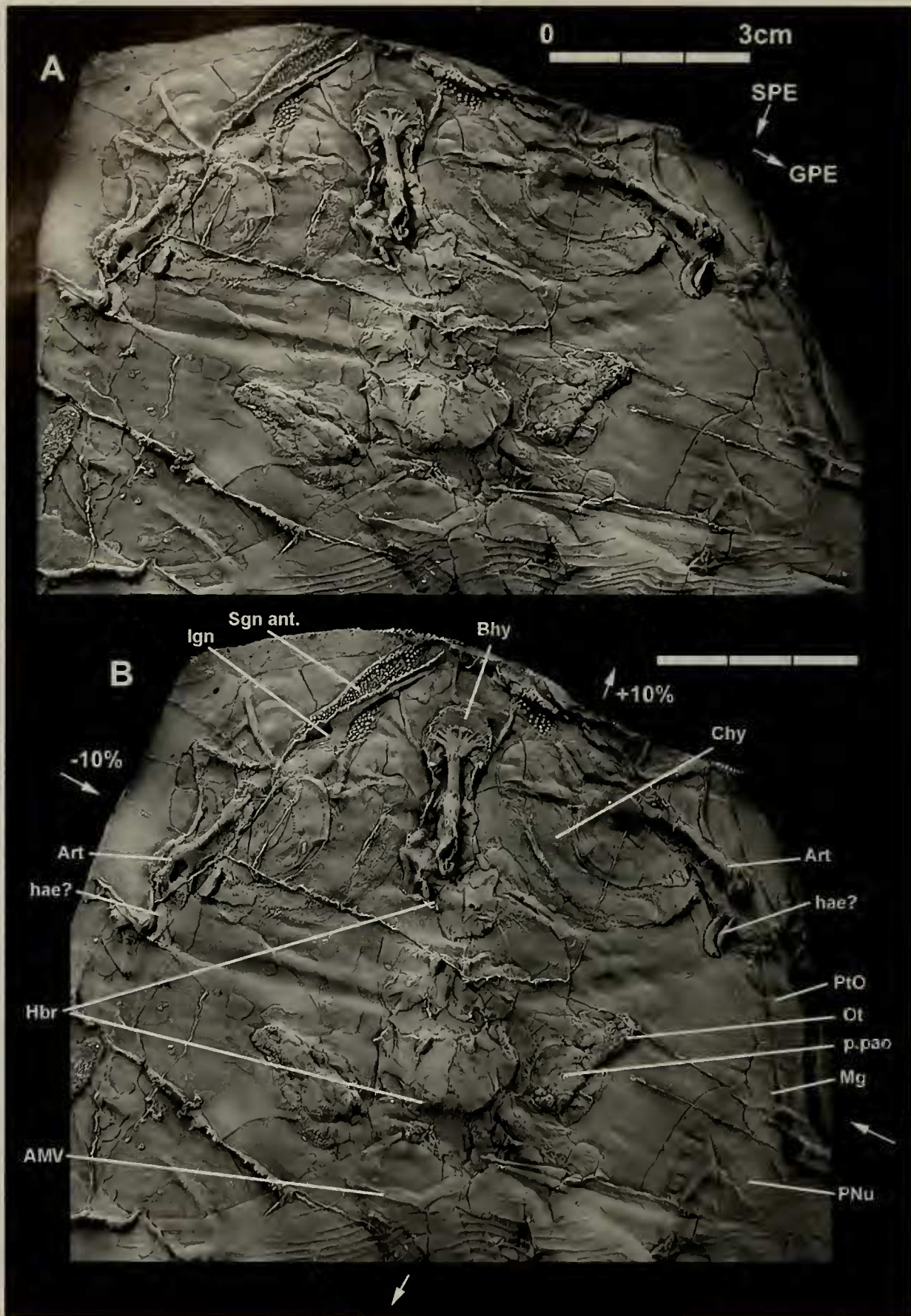


Figure 11A, B. *Cowralepis mclachlani* n. gen. and sp. AMF127156, ventral surface of head shield and anterior margin of ventral trunk shield, A) before digital modification; GPE and SPE indicate directions of Greatest and Shortest Principal Extension; B) after digital modification; arrows indicate direction and % of correction applied. (cf. Fig. 12B-D for stereo pairs of basihyal, articulars and ?hyoid arch element). Latex cast whitened with ammonium chloride sublimate.

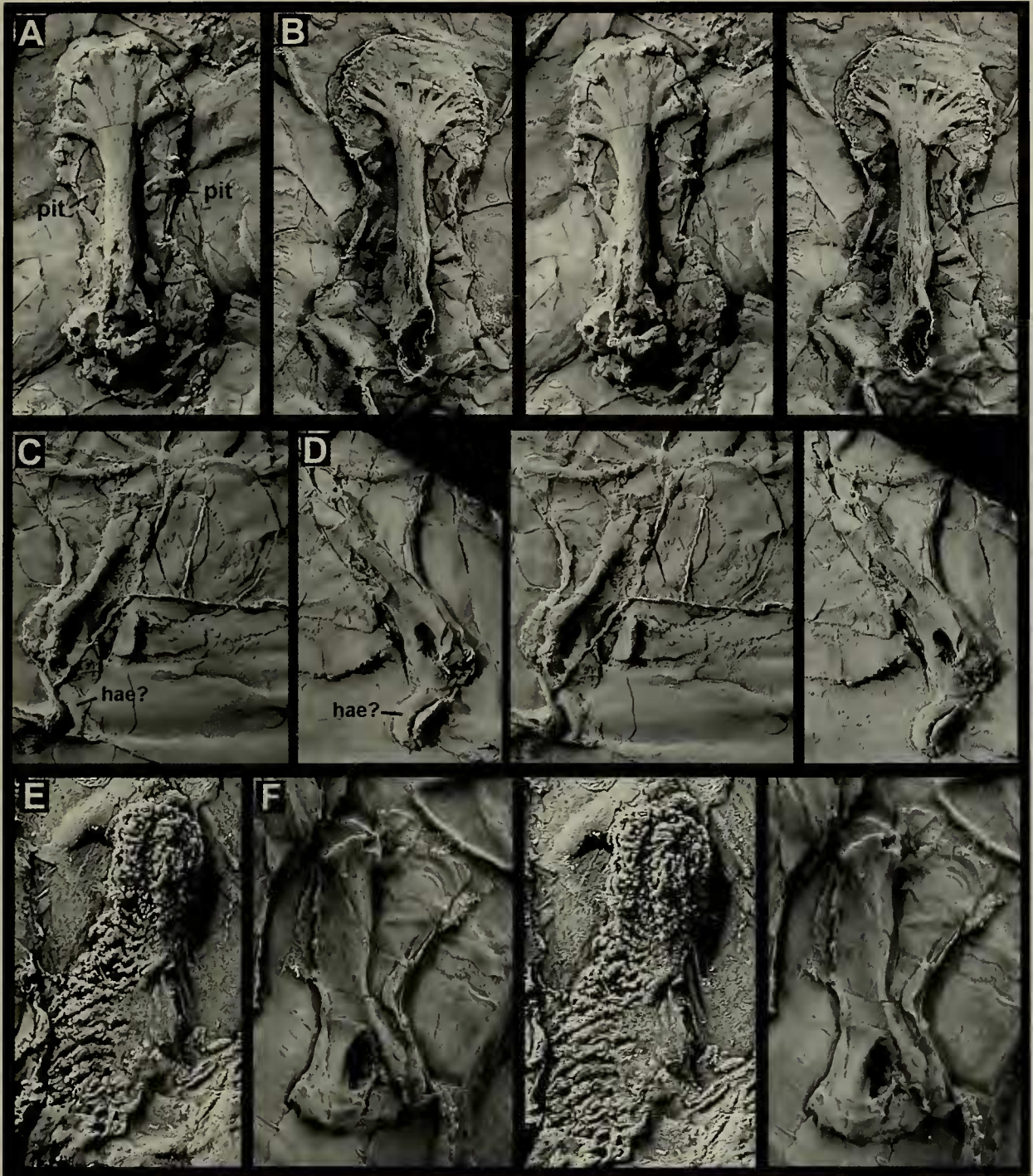


Figure 12A-F. *Cowralepis mclachlani* n. gen. and sp. Stereopair images of visceral skeletal elements and otolith. A) AMF90007b, basihyal (cf. Fig. 14A); B) AMF127156, basihyal (cf. Fig. 11A); C) right articular, ceratohyal and hyoid arch element? (cf. Fig. 9); D) AMF127156, left articular and hyoid arch element? (cf. Fig. 9); E) AMF96779, left otolith, ventral view; F) AMF96783, left articular. Latex casts whitened with ammonium chloride sublimate.

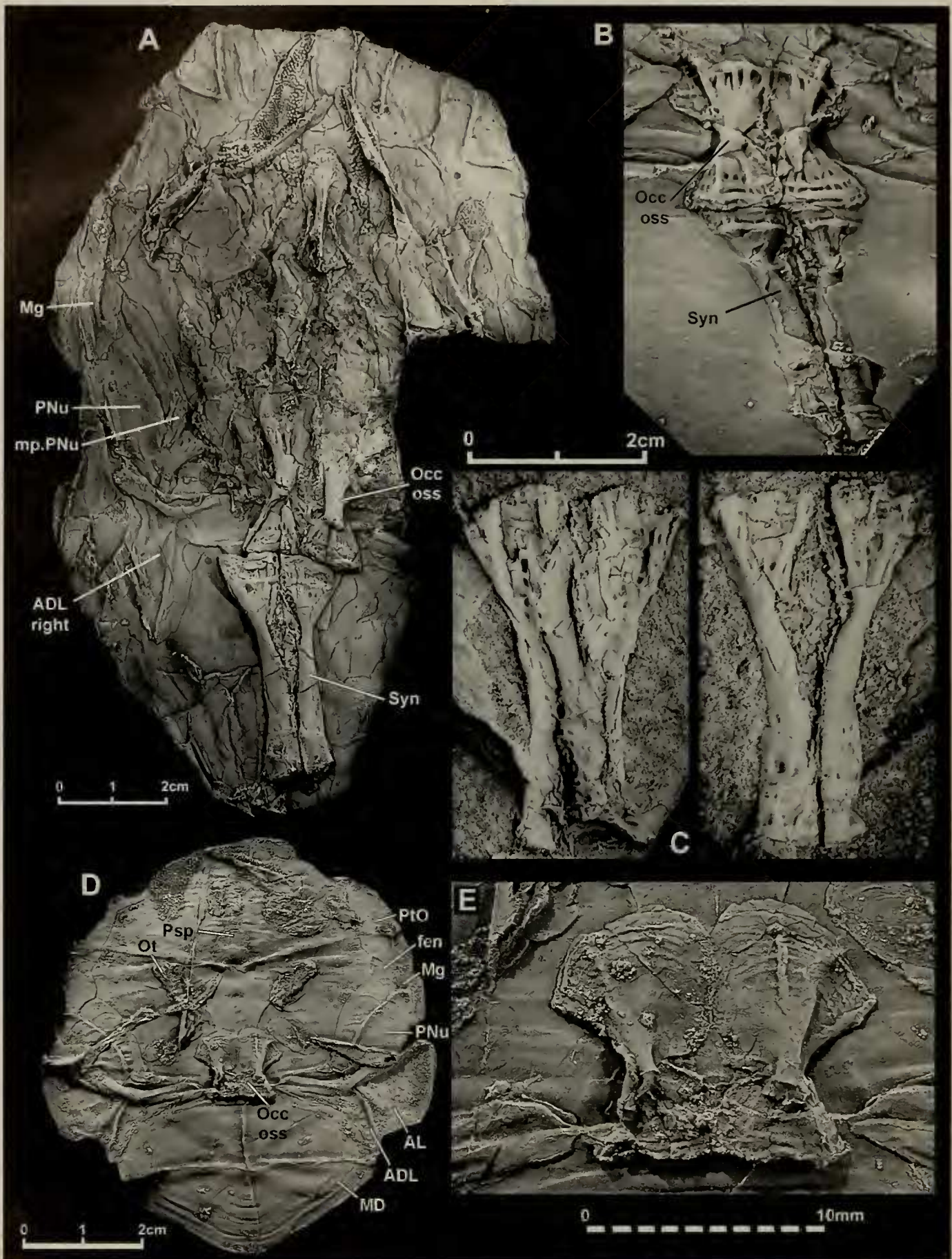


Figure 13A-E. *Cowralepis mclachlani* n. gen. and sp. Occipital and synarcual ossifications. A) AMF96751, head and trunk shields, ventral view; ventral shield lost, exposing axial skeleton; B) AMF103763, occipital ossification and synarcual, ventral view; C) AMF96753, isolated synarcual; dorsal (left) and ventral (right); D) AMF96785, juvenile dorsal shield, ventral view showing occipital ossification; synarcual lost. E) detail, ventral view. Latex casts whitened with ammonium chloride sublimate.

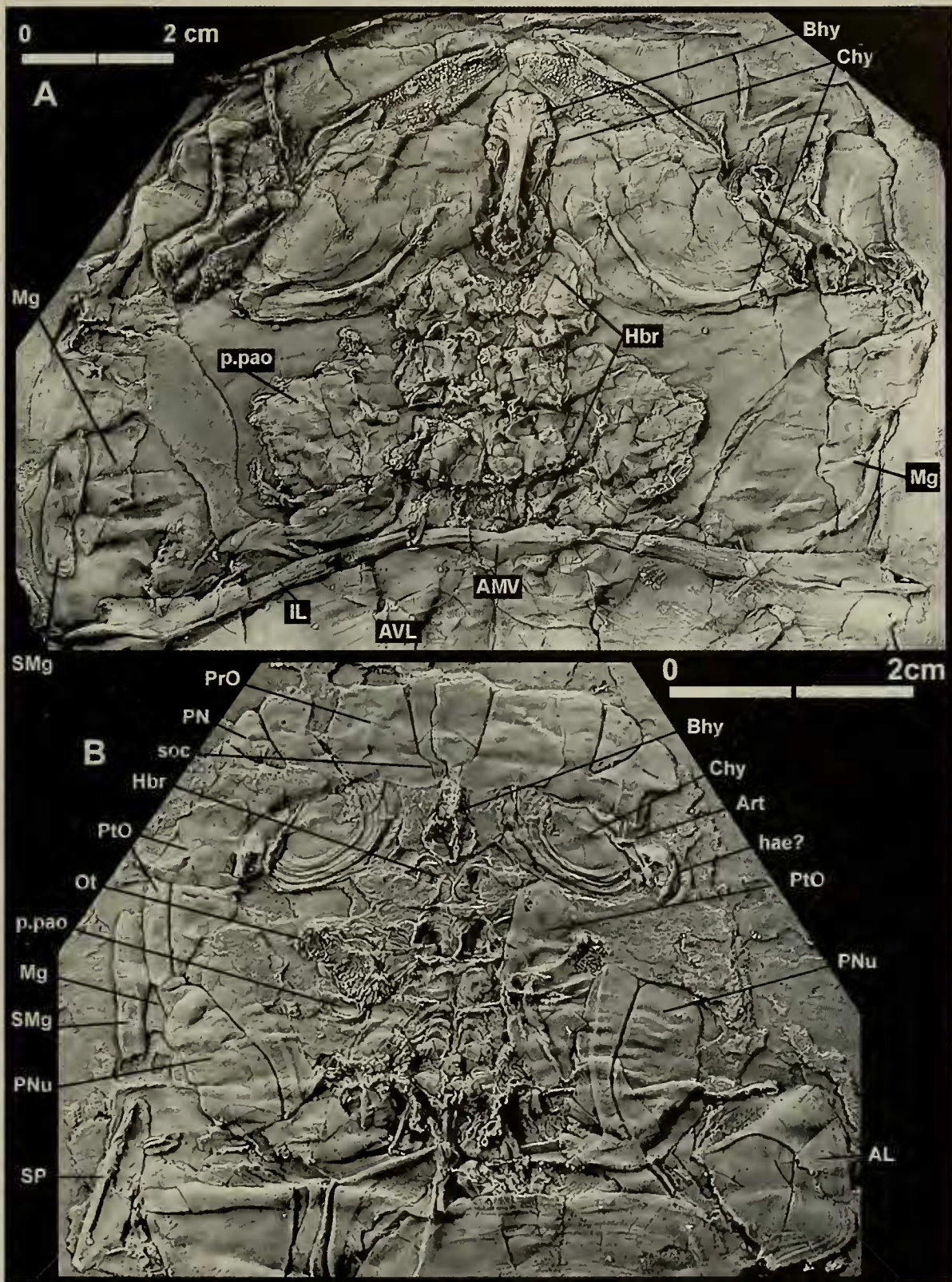


Figure 14A, B. *Cowralepis mclachlani* n. gen. and sp. A) AMF90007b, head shield of large individual, ventral view, showing all gnathal and visceral elements in association; B) AMF103776, smaller individual, head in dorsal view, Nu lost, exposing visceral branchial skeleton and otoliths in dorsal view, surrounded by circum-nuchal plates. Latex casts whitened with ammonium chloride sublimate.

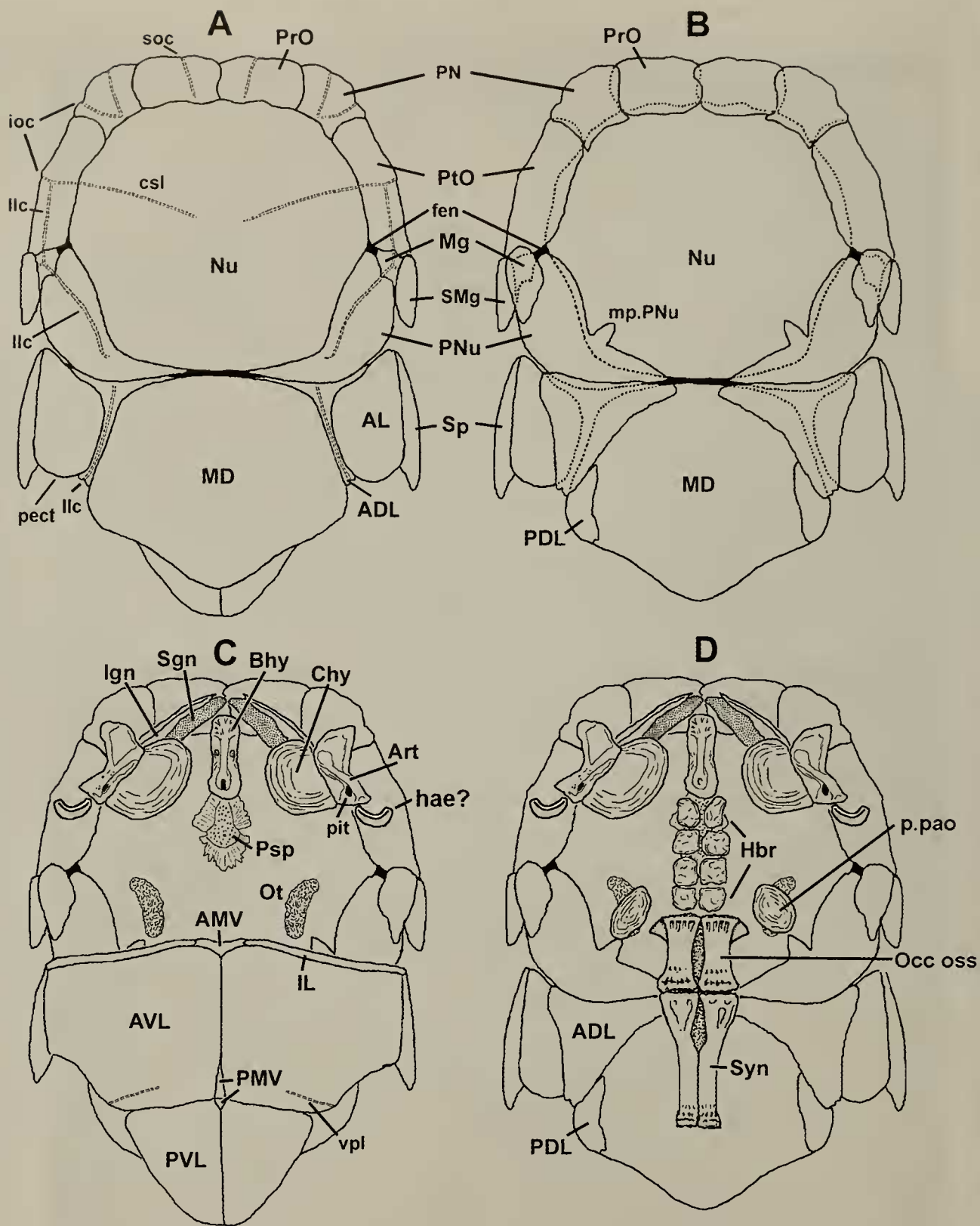


Figure 15A-D. *Cowralepis mclachlani* n. gen. and sp. A) reconstruction of craniothoracic armour, dorsal view; B) reconstruction of dorsal shield, ventral view (ventral shield omitted) showing overlap relationships of dorsal plates; C) reconstruction of craniothoracic armour, ventral view, showing gnathal elements, parasphenoid, otoliths, etc; D) reconstruction of dorsal shield, ventral view (ventral shield omitted) showing hypobranchials, occipital ossification and synarcual.

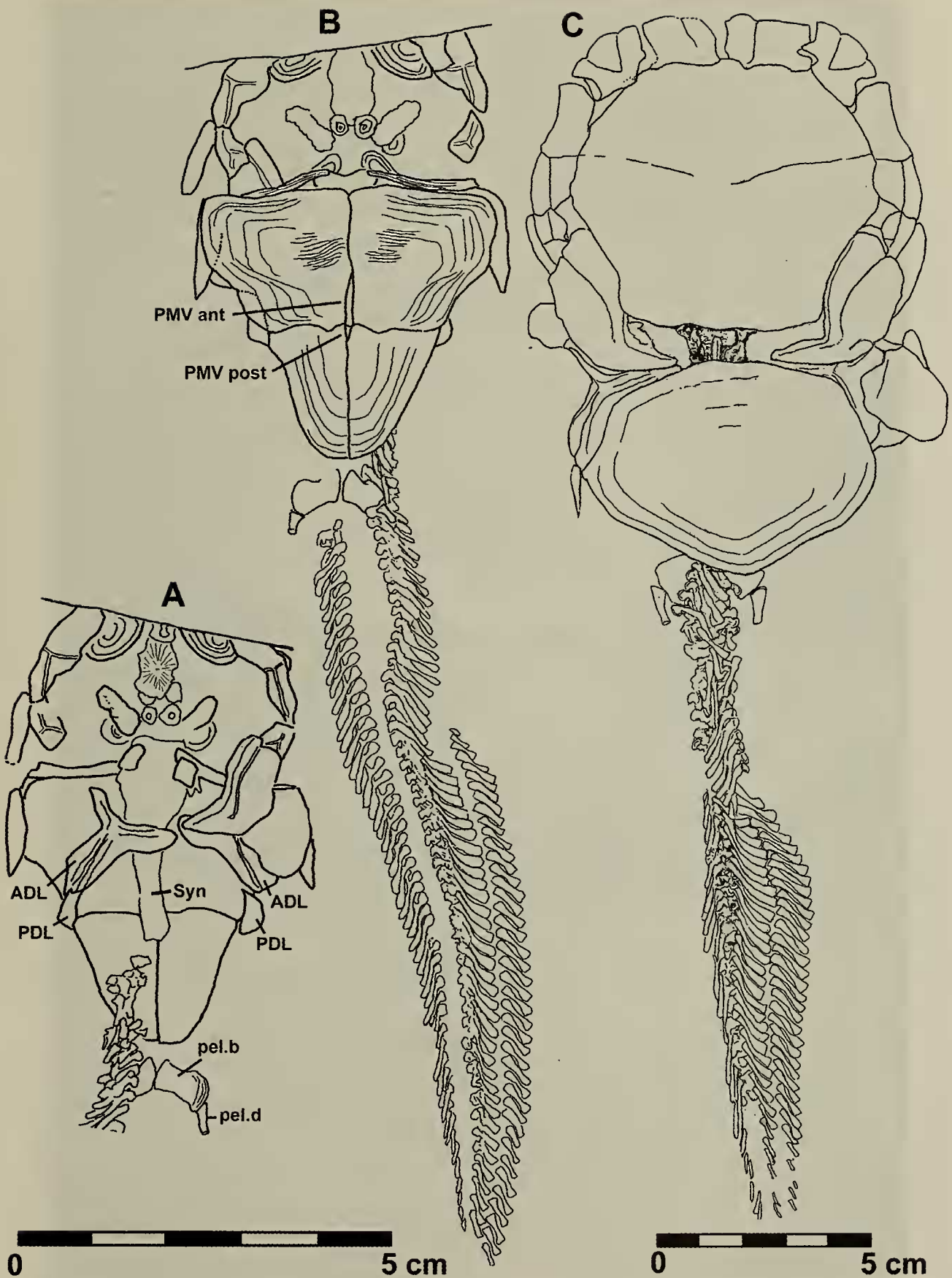


Figure 16A-C. *Cowralepis mclachlani* n. gen. and sp. A) AMF96764, dorsal view; Nu and MD plates lost, exposing ventral elements; B) AMF96765, counterpart showing ventral shield, pelvic fins and complete vertebral column; C) AMF90004, dorsal view. Both specimens digitally modified (to correct for tectonic deformation) and drawn to same length to illustrate the relative lengths of dermal armour/tail in smaller and larger individuals of *Cowralepis*.

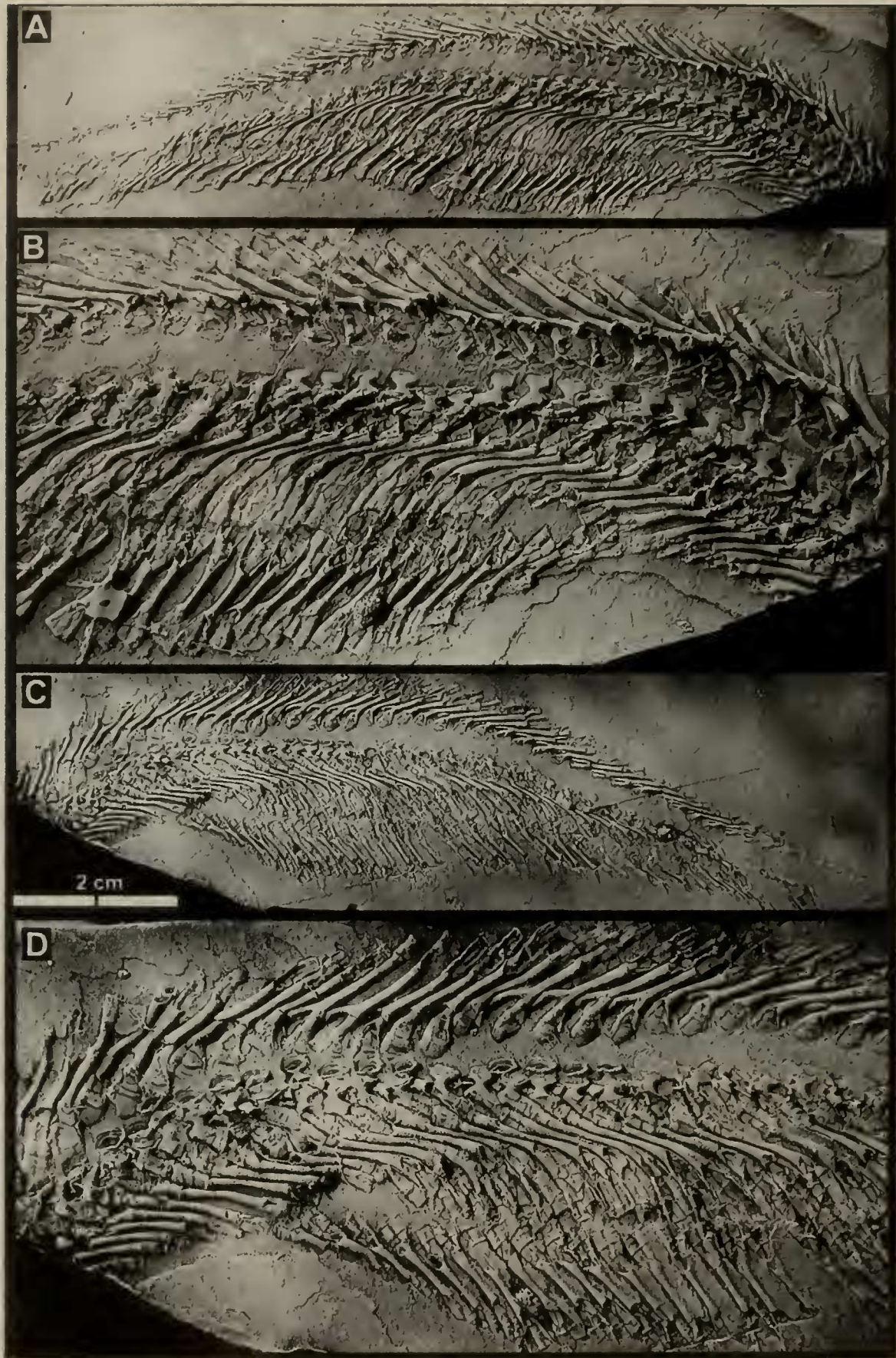


Figure 17A-D. *Cowralepis mclachlani* n. gen. and sp. Caudal fin. A, B) AMF90048a, caudal fin seen from right; B) detail of anterior region; C, D) AMF90048b, same caudal fin seen from left; D) detail of anterior region. Latex casts whitened with ammonium chloride sublimate.

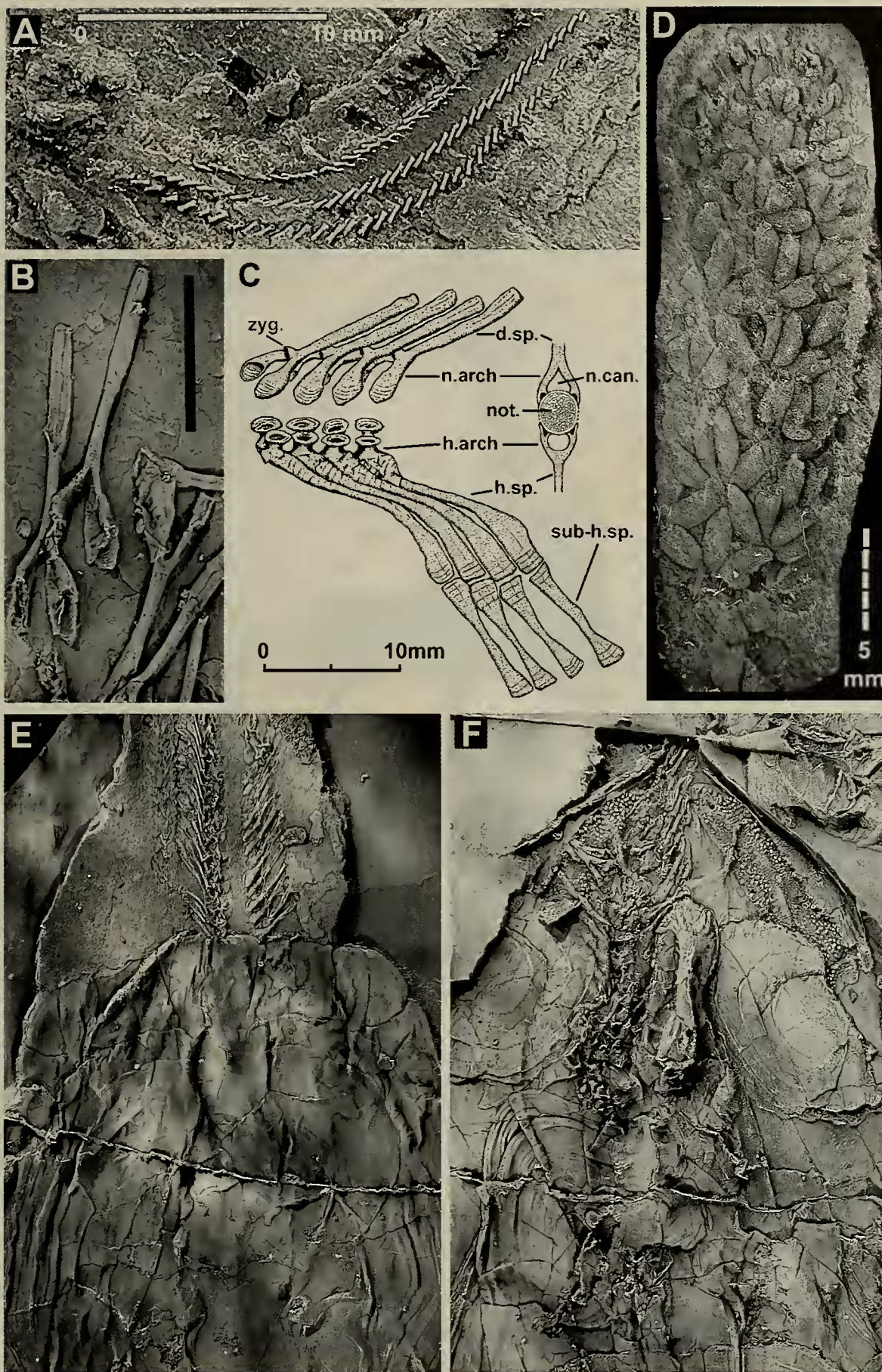


Figure 18A-F. *Cowralepis mclachlani* n. gen. and sp. A) AMF127159, juvenile vertebral column; B) AMF127154b, isolated neural arcualia; C) neural and haemal arcualia reconstructed from AMF90048 (cf Fig. 17); D) AMF127151a, egg sac from Merriganowry; E) AMF90011a, dorsal shield with smaller *Cowralepis* disappearing under anterior margin; F) AMF90011b, head shield in ventral view showing smaller *Cowralepis* inside buccal cavity (cf. Fig. 19 for interpretation). Latex casts whitened with ammonium chloride sublimate.

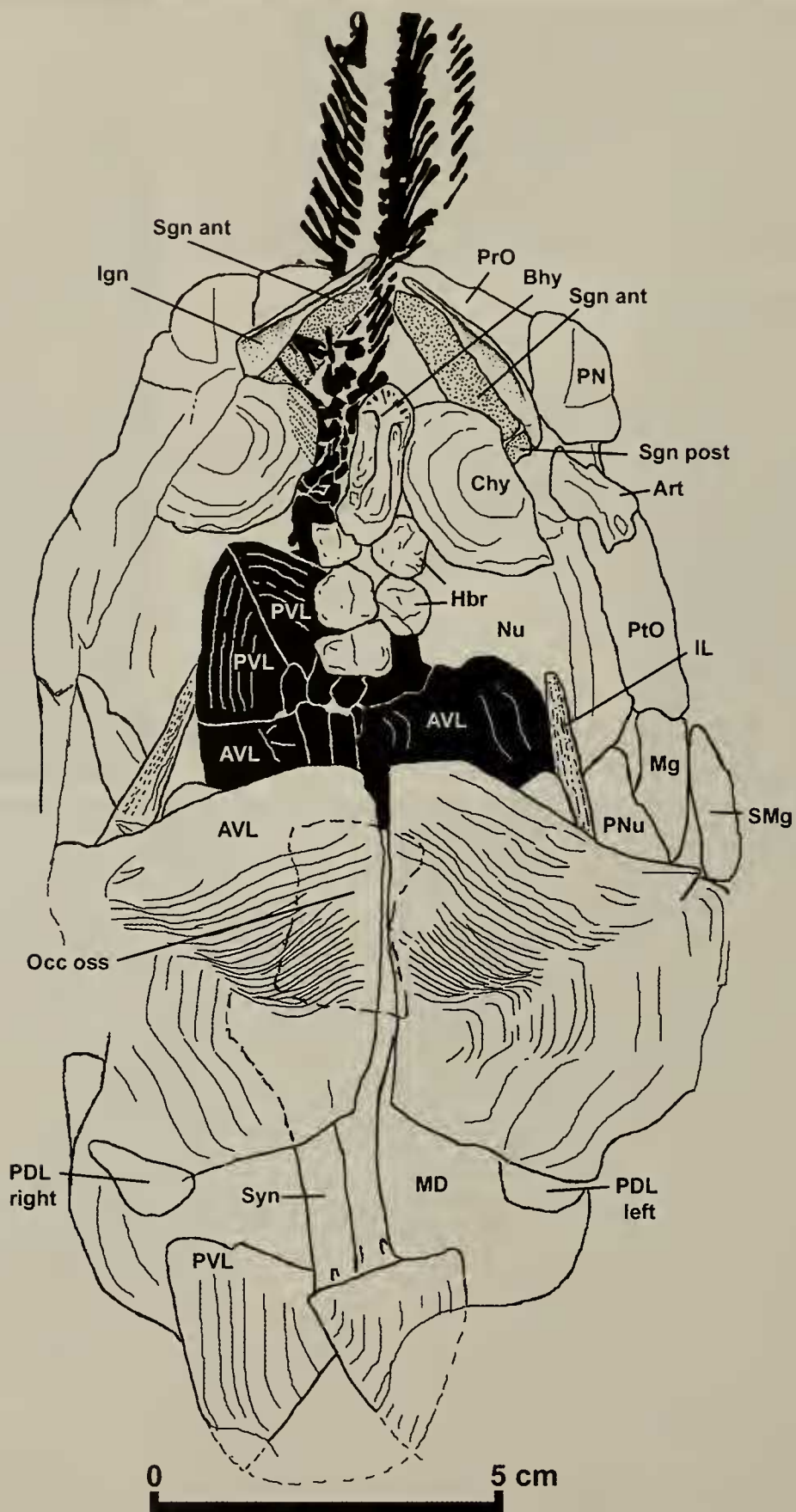


Figure 19. *Cowralepis mclachlani* n. gen. and sp. Combined sketch of the dorsal and ventral surfaces in AMF90011a, b. (cf. Fig. 18E, F). This individual appears to have died in the act of swallowing another *Cowralepis* individual that was too large, fortuitously providing invaluable information on the spatial relationships of the gnathal and branchial skeletal elements in *Cowralepis mclachlani*.

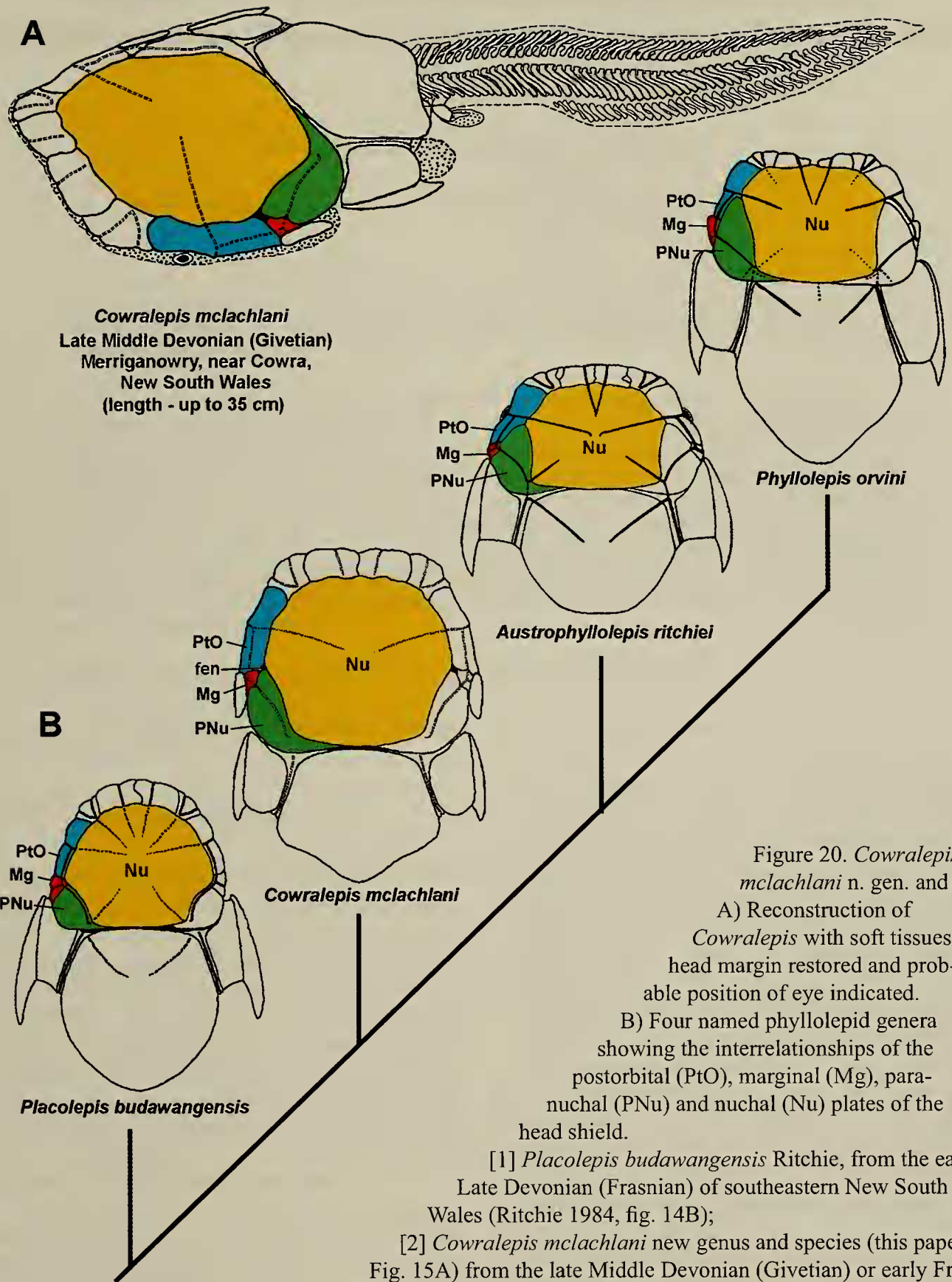


Figure 20. *Cowralepis mclachlani* n. gen. and sp.

A) Reconstruction of *Cowralepis* with soft tissues of head margin restored and probable position of eye indicated.

B) Four named phyllolepid genera showing the interrelationships of the postorbital (PtO), marginal (Mg), paranuchal (PNu) and nuchal (Nu) plates of the head shield.

[1] *Placolepis budawangensis* Ritchie, from the early Late Devonian (Frasnian) of southeastern New South Wales (Ritchie 1984, fig. 14B);

[2] *Cowralepis mclachlani* new genus and species (this paper Fig. 15A) from the late Middle Devonian (Givetian) or early Frasnian of central west New South Wales;

[3] *Austrophyllolepis ritchiei* Long from Mt Howitt, Victoria, originally dated as Frasnian, now thought to be Givetian (Young, pers. comm.). Long's reconstruction of *A. ritchiei* (1984, fig. 7A); digitally modified to correct for tectonic deformation at Mt Howitt.

[4] *Phyllolepis orvini* Heintz, from the Late Devonian (Famennian) of East Greenland (after Denison, 1978, fig. 29).